

Orientation and Communication in Arthropods

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The evolution of communication and the communication of evolution: The case of the honey bee queen pheromone

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Summary. Intraspecific chemical communication by means of pheromones is widespread in arthropods and is believed to have played a particularly important role in the evolution and the efficiency of social forms of life that have developed in several insect species. Using the honey bee queen pheromone as an example, this chapter discusses several ways in which the study of the evolution of chemical communication can potentially contribute to the resolution of a number of questions of vital importance for a better understanding of the evolution of sociality.

Introduction

Chemical communication is widespread in insects and has often reached impressive levels of sophistication even in solitary insects (*Drosophila*: Mayer and Doolittle, 1995; Moths: Ferveur et al., 1996; Kaissling, 1977; Schneider, 1984; Svensson 1996). In social insects, where communication between the members of a colony is by far more frequent and more critical than in solitary insects (Bell and Cardé, 1984; Free, 1987; Hölldobler and Wilson, 1990; Agosta, 1992; Winston, 1992), chemical communication plays a particularly significant role. For queens of many social insect colonies that need to rapidly and efficiently influence the behaviour of thousands of workers, chemical communication has perhaps no substitute. The honey bee *Apis mellifera* has been the subject of intense investigation in this regard (Bell and Cardé, 1984; Free, 1987; Winston, 1987; Winston and Slessor, 1992). We shall therefore use the honey bee queen pheromone as an example to highlight several general issues concerning the evolution of chemical communication. We will discuss several testable hypotheses that might contribute to our understanding of the evolution of pheromone-based communication. The aim of this chapter is to try to make the point that the evolution of chemical communication in social insects may communicate to us new insights concerning the evolution of sociality itself.

The honey bee queen pheromones

The honey bee queen produces a host of chemical substances that influence the behaviour and physiology of the workers in her colony. Because each colony consists of a single queen and many thousand workers, communication between the queen and her workers is, as expected, primarily mediated by chemicals. The well known effects of queen pheromones on workers include rapid detection of the presence or absence of the queen. A retinue of some eight to 10 workers, the composition of which changes every few minutes, feed and lick the queen and thereby acquire the queen pheromones and pass them on to other workers. The pheromones also inhibit the development of worker ovaries and stimulate building and foraging activities. Workers of a queen-right colony almost never lay eggs. Instead, they engage in building combs, feeding the larvae, grooming and feeding the queen, protecting the hive from intruders, foraging, and storing honey and pollen. The nearly complete sterility of the workers and their devotion to non reproductive activities, once considered paradoxical, are now interpreted as a strategy to maximize their "indirect fitness". By enhancing the queen's reproductive success (i.e., her "direct fitness"), workers enhance the transmission of their own genes, because their mother's offspring share with them many of these genes.

Which of the workers' responses are mediated by which subset of the chemical repertoire of the queen is not entirely clear. Indeed, the queen's chemical repertoire itself remains only partially known. However considerable progress has been made in recent years. Winston and Slessor (1992) have succeeded in identifying five of the most essential components of the queen pheromone which together elicit most of the important behavioural responses observed in the workers. One queen equivalent of this so-called queen mandibular pheromone (QMP) consists of about 200 μg of 9-keto-(E)2-decenoic acid (9ODA), about 80 μg of 9-hydroxy-(E)2-decenoic acid (9-HDA), of which about 56 μg is the (-) optical isomer and about 24 μg the (+) optical isomer, about 20 μg of methyl *p*-hydroxybenzoate (HOB) and about 2 μg of 4-hydroxy-3-methoxyphenylethanol (HVA) (Fig. 1). The latter two aromatic compounds are minor and, indeed, somewhat unexpected components. The aliphatic 9-ODA and 9-HDA are the major components whose involvement in the effects of the queen pheromones on worker bees has been known for a long time.

Queen control or queen signal?

The role that the queen's pheromones play in the workers' physiology and behaviour is evident from the finding that the various responses of the workers described above disappear upon removal or death of the queen. Most importantly from an evolutionary point of view, in the absence of the

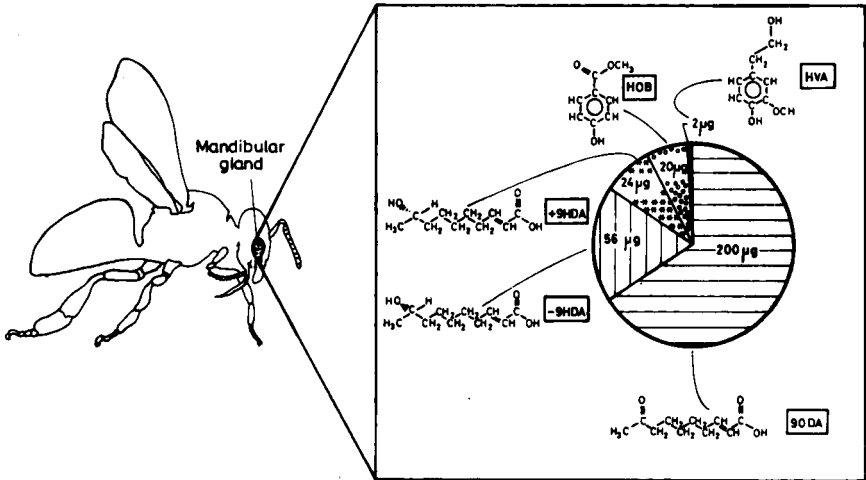


Figure 1. The queen mandibular pheromone preparation, containing well-defined amounts of five of the most important components of the mandibular gland secretion, elicits most of the responses expected from workers. See text for expansion of the names of the components.

queen, worker ovaries begin to develop and workers begin to lay small numbers of haploid eggs. Not surprisingly, this observation has been interpreted to mean that the pheromones are used by the queen to *control* the workers, *prevent* them from laying eggs and *force* them to build combs, forage and do all of those things that they do in the presence of the pheromone. Intrinsic to this concept of *queen control* of workers is the hidden assumption that the pheromone not only makes the workers do what they would not have done in the absence of the pheromone, but also that the pheromone makes the workers do what is *not good* for them in an evolutionary sense. In other words, the queen pheromone is thought to make the workers behave in a manner that is contrary to their inclusive fitness (= direct fitness + indirect fitness).

Keller and Nonacs (1993) have questioned this assumption. They argue that pheromonal queen control which can make the workers act against their own best interests has never really been demonstrated, and cannot possibly evolve. They argue that queen control has never really been demonstrated, because all phenomena hitherto interpreted as queen control bear alternative interpretations, the most logical of which is that workers are actually acting in a manner that maximizes their inclusive fitness. But can refraining from laying eggs be a way of maximizing their inclusive fitness? Yes, and for several reasons. First, as already mentioned above, the queen is the workers' mother and her offspring are therefore their siblings. Second, a healthy queen is by far a superior egg layer compared to any worker. Third, queens can lay both haploid and diploid eggs, whereas the

workers (which are incapable of mating), can only lay male destined haploid eggs. Fourth, workers should prefer the queen eggs, even when it comes to haploid eggs, because when the queen is multiply mated, as is most often the case in nature, each worker is more closely related to the queen's sons (who would be related to her by 0.25) than she is to another worker's sons (who would only be related to her by 0.125 if the worker in question is her half sister) (Ratnieks, 1988, 1990; Ratnieks and Visscher, 1989). Keller and Nonacs (1993) argue that pheromonal queen control cannot possibly evolve, because a situation where the queen accomplishes what is good for her at the expense of the workers who are forced to accept what is not so good for them, is evolutionarily unstable. In such a situation, workers would be expected to evolve defenses against queen control and revolt against her hegemony. A mutation in the workers that can ignore the queen pheromone would be favoured by natural selection as it would then be able to accomplish what is good for the worker, from the point of view of its own inclusive fitness. If it is in the best interests of the workers to leave egg laying to the queen when she is present and healthy, but efficiently detect the absence of the queen or any deterioration in her health and start laying their own eggs, we would still see the same phenomena in response to the queen pheromone as we do now. However, the queen pheromone should then be thought of as a *signal* that the workers use to decide when they should let the queen reproduce and when they should take over egg laying on to themselves. Whether the queen is controlling the workers, making them do what is good for her but not so good for them, or whether the workers are using the queen pheromone as a signal to do what is best for them, which also happens to be approximately what the queen wants them to do, are not equivalent and it is not a matter of semantics either.

At the heart of this genuine dichotomy in the nature of chemical communication is a question of fundamental importance to the study of social evolution: are both queens and workers simultaneously maximizing their respective inclusive fitnesses, leading to an evolutionary stable equilibrium, or are queens successfully manipulating workers into acting against their inclusive fitness so that social insect colonies are inherently evolutionarily unstable? Keller and Nonacs favour the former interpretation which seems reasonable and might perhaps represent a new level of maturity in our approach to the study of social insect biology. The significance of this shift in interpretation of the function of the queen pheromone for our understanding of both the evolution of chemical communication and the evolution of sociality, is not trivial. A few additional comments about the view championed by Keller and Nonacs are perhaps necessary before we can fully appreciate this shift. Keller and Nonacs do not entirely rule out the possibility of pheromonal queen control at the expense of worker inclusive fitness. Their contention is that the available evidence can equally well be interpreted (and perhaps better interpreted, in conjunction with the argument of evolutionary stability) as a case of the workers using the queen

pheromone as a signal to achieve their own interests. Indeed, they proceed to make several testable predictions that might help decide between the theory of pheromonal queen control and the signal hypothesis.

(i) The inhibitory effects of the queen on worker reproduction should be independent of her egg laying ability, as it would then prove that workers are being suppressed even when the queen is not such a good egg layer. The signal hypothesis, on the other hand, predicts that the level of suppression of worker reproduction be proportional to the queen's egg laying ability.

(ii) Queens laying only male-destined eggs should exhibit the same level of inhibition on worker reproduction as do queens producing both sons and daughters, as this would prove that workers are being inhibited both when it is good and when it is bad for them to reproduce on their own. The signal hypothesis, however, predicts that worker reproduction should be inhibited more strongly when the queen is producing daughters than when she is producing only sons.

(iii) In multi-queen colonies (as is often the case in ants), inhibition of worker reproduction should increase as queen number increases, because more pheromone from more queens should cause more inhibition. The signal hypothesis suggests, instead, that workers should be more likely to reproduce on their own when there are many queens, as the relatedness of the queens' offspring to themselves decreases with increase in queen number.

(iv) When there is a genuine queen-worker conflict such as is apparent in the optimal sex investment ratio (Trivers and Hare, 1976), the queen's preferred optimum should prevail over the workers' preferred optimum. A 1:1 female to male ratio (optimum for the queen), rather than a 3:1 ratio (that is optimum for the workers in a monogynous colony with a singly mated queen), would suggest that the queen successfully forces workers to act in ways that maximize her own interests at the expense of the workers' interest.

Because these predictions remain to be tested, Keller and Nonacs do not rule out the possibility of genuine queen control. They suggest, however, that whereas the term "pheromonal queen control" be reserved for situations where there is evidence that "workers or subordinate queens are chemically manipulated by queen(s) into pursuing actions that are contrary to their inclusive fitness", the term "pheromonal queen signal" be used for situations where "workers or subordinate queens react to queen pheromones in ways that increase their (and possibly the queens') inclusive fitness", and the term "pheromonal queen effect" be used "where the changes in the workers' or subordinate queens' behaviour have an unknown consequence on their inclusive fitness". It might be worth noting that Keller and Nonacs keep referring to subordinate queens because they are also concerned with many ant species where, unlike in case of the honey bee colony, there are several queens per colony. There is often a clear dominance hierarchy among the queens in polygynous ant colonies so that dominant queens

must also influence subordinate queens in much the same way as they do workers. The nomenclature suggested by Keller and Nonacs implies that all effects of the queen pheromone on workers and subordinate queens should begin their life (in the literature) as pheromonal queen effects until they attain the status of either pheromonal queen control or pheromonal queen signal, after the appropriate experiments have been carried out and one or the other criterion satisfied. It may well happen that what starts out as pheromonal queen effect may sometimes end up as pheromonal queen control and at other times as pheromonal queen signal, depending on the particular effect being considered and on the particular species of social insect being investigated.

This dichotomy between *control* and *signal* in chemical communication implies a similar dichotomy between *exploitation* and *mutualism*, between evolutionary *instability* and *stability* in all relations between queens and workers or dominant and subordinate queens in social insect colonies (see Markl, 1985, for an illuminating discussion of communication dyads with different costs and benefits to senders and receivers of information). Understanding the evolution of chemical communication between queens and workers or subordinate queens will therefore have much to communicate to us about the evolution of sociality itself. When considerable further progress has been made in our understanding of chemical communication between queens and workers and between dominant and subordinate queens, and we will have discovered a large number of queen pheromonal effects and transferred most of them into either the control category or the signal category, we may be able to prepare a tally of cases of queen control versus queen signal in different species and with reference to different kinds of pheromonal effects, a tally that would promise to reveal a great deal about the nature of evolution of chemical communication and of evolution of sociality itself. In particular, it should help resolve the issue of exploitation versus mutualism, a dichotomy that has long plagued discussions of the evolution of eusociality (see Lin and Michener, 1972; Alexander, 1974; Trivers and Hare, 1976; Alexander and Sherman, 1977; Gadagkar, 1985). It would also be most relevant to a possible resolution of the virtually neglected question of whether or not selfishness and perhaps even solitary life can reemerge from the highly eusocial state (Gadagkar, 1997b, c).

Queen pheromone as poisonous prestige and handicap?

Zahavi and Zahavi (1997) have suggested that the queen pheromone is a poison, the possessing of which is a handicap, but that it is precisely the "prestige" associated with the ability to withstand this handicap that makes it possible for the queen to influence the workers, and at the same time to make it advantageous for the workers to help the queen. Because this sug-

gestion may seem extraordinary to most of us, it is necessary to digress momentarily from our discussion of the honey bee queen pheromone and see it in the backdrop of Zahavi's handicap principle and his ideas about the evolution of honest signals (Zahavi, 1975, 1977, 1990, 1993). Zahavi is the most ardent individual selectionist around today who insists that an honest attempt should be made to explain all known biological phenomena in the framework of individual selection. He sees in the theory of kin selection the same problem of instability that most of us recognize in group selection. The cause of instability is, of course, the possibility that cheaters can garner the advantage of altruism exhibited by some members of the group without any investment on their own part. This would give an advantage to the cheaters who would increase in frequency and finally drive the altruists to extinction. True, the problem of such instability is less serious in the case of kin selection as compared to group selection. But there is no denying the fact that the problem of cheaters does not exist in the case of individual selection, simply because nobody is supposed to be altruistic; everybody is doing the best he or she can do under the circumstances. If a viable explanation can be found within the framework of individual selection for why it is advantageous to the honey bee worker to help the queen, rather than try to reproduce by herself, then it would certainly be more satisfactory than even a kin selectionist explanation that relies on the indirect advantage of helping. It is the extreme rarity of people who are willing to pursue an individual selectionist explanation to its logical conclusion, especially with respect to worker altruism in highly eusocial insects, that makes the Zahavis' point of view so valuable.

For over two decades, Zahavi (1975, 1977) has championed (amidst much skepticism) the so-called handicap principle. Initially, Zahavi's intention was to provide a satisfactory explanation for the elaborate and exaggerated secondary sexual characters and displays usually shown by males (such as the train of the peacock, the antlers of deer, or the songs of some birds). These traits are supposed to have evolved by sexual selection, a mechanism that even Darwin thought best to keep distinct from natural selection (Darwin, 1871). A widely accepted mechanism for the action of sexual selection is Fisher's run-away selection (Fisher, 1930) which postulates that, initially, the secondary sexual characters correlated well with male quality and hence females that had a preference for males with the elaborate traits had an advantage over other females. Fisher argued that, later in evolution, the very fact that females prefer elaborately ornamented males gives an added advantage to the males possessing the ornaments so that selection for the male secondary sexual characters goes beyond the level predicted by their correlation with fitness. In other words, male ornaments become a handicap, making it, for example, harder for their bearers to escape from predators. However, males with such characters are not easily eliminated by natural selection because females show a preference for such males, a preference that has persisted from the period when male

ornamentation was correlated with male fitness. As opposed to Fisher (1930), Zahavi (1975) has argued that females will not prefer traits that are not correlated with fitness just because these traits used to be correlated with fitness at some time in the past. The handicap, Zahavi argues, is a true indicator of male quality, because if a male has survived despite the disadvantages involved, then he must possess very good genes. In other words, the handicap is an honest, reliable signal of male genetic quality. Although early models appeared to show that Zahavi's idea cannot work (Davis and O'Donald, 1976; Maynard Smith, 1976; Kirkpatrick, 1986), subsequent, more realistic models show that Zahavi's handicap principle is indeed plausible (Kodric-Brown and Brown, 1984; Nur and Hassan, 1984; Grafen, 1990a, b).

Apart from providing a potential explanation for exaggerated male secondary sexual characters, the handicap theory leads to another important conclusion, namely, that communication signals must be costly in order to be honest. If a peacock's quality is assessed by the length of his tail, then there is no way an inferior peacock can bluff and indicate a higher than true quality, because inferior peacocks can neither grow nor carry long tails. Thus, in principle, any signal can be trusted to be an honest signal if it is costly, because no male can provide such a signal unless he is capable of carrying it despite the handicap. If male quality were to be inferred by the females through some inexpensive signal that anybody could give, cheaters would get away by sending signals indicating a quality higher than that they actually possess, and the signaling system would soon break down (Zahavi, 1987, 1993). In addition to its compelling logic, and many convincing examples discussed by Zahavi, the prediction that a signal can only be honest if it is costly has already been verified through formal evolutionarily stable strategy (ESS) models (Grafen, 1990a, b; Godfrey, 1991; Maynard Smith, 1991; Johnstone and Grafen, 1992a, b).

The idea that only costly signals are honest signals, together with the handicap hypothesis from which this idea has been derived, lead Zahavi to the concept of prestige as a reward for altruism. This concept, based on his investigations of cooperative breeding in the Arabian Babbler (Zahavi, 1990, 1995), is radically different from all of the theories proposed previously. Because group selection, kin selection, as well reciprocal altruism (Trivers, 1971; Wilkinson, 1988), are all susceptible to cheating, Zahavi rejects them as possible explanations for why babbler helpers actually help. Instead, he explains the evolution of helping in babblers through "old fashioned" individual selection. He argues that all apparent cases of altruism are, as a matter of fact, acts of selfishness. By investing in the welfare of the group, taking risks in defending the group and behaving in apparently altruistic ways, individuals increase their prestige in the group. This prestige serves as an honest signal indicating the quality of this individual as a collaborator and as a rival in intra-group conflicts. The social prestige thus acquired helps the individual to increase its chances to

reproduce, when the opportunity to do so arises. Zahavi's main evidence for this idea comes from his observation that his babblers are highly motivated to help, and do not ever try to get the benefits of group living without investing in its welfare. Indeed, babblers compete with each other in allo-feeding, in feeding the nestling, and in performing sentinel duties (Zahavi, 1990). Moreover, dominants often prevent subordinates from helping the group, thus keeping this privilege to themselves. If social prestige indeed helps the individual to increase its direct fitness, then this individual's altruism must be considered as one that has been motivated by a selfish design. Individual selection would thus be sufficient to explain the evolution of this type of altruism. None of the other theories, namely, group selection, kin selection and reciprocal altruism, can explain why there should be competition for being altruistic.

Looking at honey bees from their unabashed, individual selection bias, Zahavi and Zahavi (1997) argue that, given the inevitable superiority of the honey bee queen over the workers, the best that a worker can do is to bide her time until an opportunity arises for her to lay haploid eggs and produce some sons. But very few workers will actually get that chance. Zahavi and Zahavi (1997) suggest that the probability of getting that chance can be increased not by sulking and refraining from working, but, instead, by actually working for the colony and, by doing so, enhancing their prestige. In small social insect colonies, as in the babblers, the achievements of different individuals and their consequent prestige in the group can be known to all members of the colony. In a large colony such as the honey bee, however, individuals remain largely anonymous and a different mechanism to indicate prestige is required. It is here that Zahavi and Zahavi (1997) turn their attention to the honey bee queen pheromone. They suggest that the queen pheromone is a poison made by the queen to which workers are far more sensitive than is the queen herself and thus there is not much that workers can do about this. Hence, as long as the queen is alive and healthy, she will suppress them. This is equivalent to their using the queen pheromone as an honest signal to do what is best for them under the given circumstances. It is only when the queen becomes weak or she dies that the workers have a real opportunity to try to reproduce, and it is here that their prestige may come in handy.

If the queen pheromone is a poison, then workers are expected to exhibit some natural variability in their resistance to this poison. This ability can in turn be an honest signal of their quality. Like the babblers which compete with each other to perform altruistic acts, workers must compete with each other to acquire the queen pheromone, and they are indeed known to do so. Zahavi and Zahavi (1997) have also postulated that working hard for the welfare of the colony might in fact help the worker's metabolize the queen pheromone faster and hence enhance their ability to deal with the poison. To quote Zahavi and Zahavi (1997): "...the very act of working for the hive may increase the worker's ability to carry pheromone in the same way

that a college student may 'hold his liquor' better after a year spent as a construction worker than he did in his fraternity party days." The pheromone can thus be thought of as a handicap that queens and some workers (more than others) can tolerate on account of their superior physical condition. Just as the pheromone carried by the queen can be an honest signal indicating that she is better at egg laying than any worker, the quantity of queen pheromone carried by each worker can be an honest signal of how good and strong this worker is (both as a companion and as a rival) compared to other workers, a comparison that especially comes to the fore upon death of the queen. As Zahavi and Zahavi (1997) point out, the suggestion that the quantity of queen pheromone carried by an individual is a handicap which indicates prestige in a large colony and is therefore an honest signal of the individual's quality, is yet only a hypothesis, but it is an eminently testable one. Here I am not concerned with the possibility of its ultimate correctness (for idle speculation in this matter, without experiment, may be futile). Instead, I wish to examine its theoretical implications for the evolution of chemical communication and for the evolution of sociality.

Kin- and group selection versus individual selection

Let us first compare and contrast the point of view of Zahavi and Zahavi (1997) with that of Keller and Nonacs (1993) which we discussed in the previous sections. Both points of view consider the queen pheromone to be an honest signal that the workers find in their best interests to obey. But there is a subtle difference between the two points of view. For Keller and Nonacs, both queens and workers are maximizing their inclusive fitness and thus achieving a stable evolutionary equilibrium. Mutations making the workers lay some eggs in the presence of the queen will not be favoured, because the workers' inclusive fitness is maximized by suppressing their own reproduction and permitting the queen to lay eggs. For Zahavi and Zahavi (1997) it means that there is an inherent asymmetry between queen and worker (or between different workers). With the help of the queen pheromone as an honest signal, the inferior individual can correctly assess the quality of the superior individual and accept its own subordinate status, because there is nothing else that it can do. Workers fitness (direct fitness, which is all that Zahavi cares about!) may in fact be enhanced if they suppressed the queen and took over egg laying (in spite of their poor egg laying capacity), but they cannot compete with the queen in dealing with the poison that is in the pheromone. The main reason for this difference, in the arguments of Keller and Nonacs on the one hand and the Zahavi and Zahavi (1997) on the other, is that whereas the former use the framework of kin selection (maximization of inclusive fitness), the latter argue with the power of individual selection (maximization of classical individual fitness). According to Zahavi and Zahavi (1997), "the chance

the worker has to reproduce within the colony is the cement that permitted the creation of large, stable partnerships, encompassing thousands of individuals, in which the reproductive success of the individual workers depends on the success of the queen”.

Keller and Nonacs (1993), on the other hand, do not consider the possible role of individual selection. According to their theory, only kin- and perhaps group selection can explain the role that queen pheromone plays in communication. In the context of polygynous ant colonies, Keller and Nonacs worry that a queen attacking other queens chemically is also likely to affect herself, and that this is one of the reasons to take recourse to thinking of the queen pheromone not as a weapon of attack but rather as a signal. A fundamental tenet of Zahavi's theory of signal selection is, however, that no signal can be reliable and will therefore not be taken seriously by the receiver unless it is costly for the sender. Thus, the possibility that a queen using a pheromone to influence other queens may be attacking herself is not likely. Only a queen capable of withstanding the harmful effects of the pheromone can use it as a reliable signal of her superior status. Keller and Nonacs's problem arises because they are implicitly assuming that all individuals (workers as well as queens) are similar in their ability to deal with the queen pheromone, which is in stark contrast to the ideas of Zahavi.

It should be noted that Keller and Nonacs propose that true control which makes the workers act against their best interests can also evolve in the case of physical control of workers by the queens (via aggressive behaviour that is particularly common in small colonies, see e.g., Premnath et al., 1996; Gadagkar, 1997b). According to Zahavi's theoretical framework there should be no real difference between physical and chemical control. Even in cases in which queens use physical methods to influence workers, there should evolve a system of costly, honest signals that would permit the interpretation that workers are responding to some queen's characters (whatever these may be; in the case of physical control, for example, enlarged body size) as signals to do what is best for them, i.e., letting the queen lay eggs when she is strong and healthy, but taking it upon themselves to do so when the queen is not in a good shape or when she has died.

Keller and Nonacs (1993) argued, in addition, that chemical control of workers by queens cannot have evolved, because it would become prohibitively expensive for queens to stay ahead of the workers in the chemical arms race. However, they did not consider the possibility that it might also become prohibitively expensive for workers to stay ahead, and therefore it might be profitable for them to obey the queen. The implication is that if the queen were to use the pheromone to *control* the workers and force them to do what is not in their best interests, then she may not necessarily succeed, because there is no guarantee that she wins the chemical arms race. Therefore, the pheromone must be considered to be effective in influencing the workers' behaviour solely on the basis that workers use it as a *signal* to

do what is best for them. If, however, the queen pheromone is to be thought of as being not just a signal, but rather a *poison* the carrying of which is a handicap that queens can bear better than workers, as proposed by Zahavi and Zahavi (1997), then it would follow that queens inherently have an advantage over workers and should therefore be more likely to win the arms race. The assumption of inherent and inevitable differences between queens and workers is, indeed, an essential component of the individual selection argument of Zahavi and Zahavi (1997). They write: "The fact that the queen is able to raise daughters smaller and weaker than herself makes it possible for her to exploit them: it is precisely the inequality between queen and workers that limits the workers' options and makes the asymmetrical partnership so stable."

Should the Zahavis' hypothesis, proposing that the queen pheromone is a poison and thus a handicap serving to build prestige, be verified, then our picture of the evolution of chemical communication between queens and workers will be rather radically altered, and consequently our picture of the evolution of sociality will be an even more radically different one. In particular we might then be able to explain at least the maintenance of sociality in the honey bee (and perhaps other highly social insects) by individual selection without recourse to kin selection or group selection. Hence my assertion again, that our understanding of the evolution of chemical communication between queens and workers will have a great deal to communicate to us about the evolution of sociality itself.

Queen-worker dichotomy: A chicken and egg problem

Perhaps the most fascinating aspect of honey bee colonies is the differentiation of the bees into a sterile worker caste and a fertile queen caste. The question that stems from this fact relates to the possible differences between queens and workers in their pheromone blends and the mechanism of the origin of these differences. These are the questions that Plettner et al. (1996) address in a recent path-breaking paper. Workers, too, produce mandibular gland secretions that are added to the brood food and may serve as preservatives and nutrients. Instead of the two major components of the queen's secretions, namely 9-keto(E)2-deconoic acid (9-ODA) and 9-hydroxy-(E)2-decenoic acid (9-HDA), workers secrete acids hydroxylated at the 10th or ω -carbon atom, rather than the 9th or ω -1 carbon atom as in the case of the queen's acids. Instead of the queen's 9-HDA, workers secrete 10-hydroxy-(E)2-decenoic acid (10-HDA), and instead of the queen's 9-ODA, workers secrete the diacid acid derived from their 10-HDA. In other words, queens and workers differ essentially only in the position of the carbon atom that is hydroxylated. But how does this difference arise? Based on a series of experiments analyzing the fate of deuterated test compounds applied to excised queen and worker mandib-

ular glands, using gas chromatography-mass spectrometry (GC-MS), Plettner et al. (1996), have proposed the following caste-specific, bifurcated three step biosynthetic pathway for the production of these compounds (Fig. 2).

The starting point is stearic acid, an 18-carbon, straight chain, saturated hydrocarbon, which is a very common intermediate step in the oxidation of lipids (see Mahler and Cordes, 1966, for a detailed account of lipid metabolism). In the first step of the proposed pheromone biosynthetic pathway, functionalization is achieved by the addition of a hydroxyl group on either the 18th (ω) or the 17th ($\omega-1$) carbon atom. This functionalization which foreshadows the queen-worker differences depending on whether it happens at the ω or the $\omega-1$ carbon atom is, however, itself not caste-specific; both ω and $\omega-1$ functionalizations occur in both castes to about the same extent. In the second step, the 18-carbon hydroxy acids are shortened to give 10-HDA and 9-HDA by the standard chain-shortening cycles of β oxidation that normally occur during fatty acid metabolism. It is the β oxidation step that is caste-specific – queens preferentially channel the $\omega-1$ compounds and workers the ω compounds into the oxidation pathway. In the final step, oxidation of the ω or $\omega-1$ hydroxy group that was added

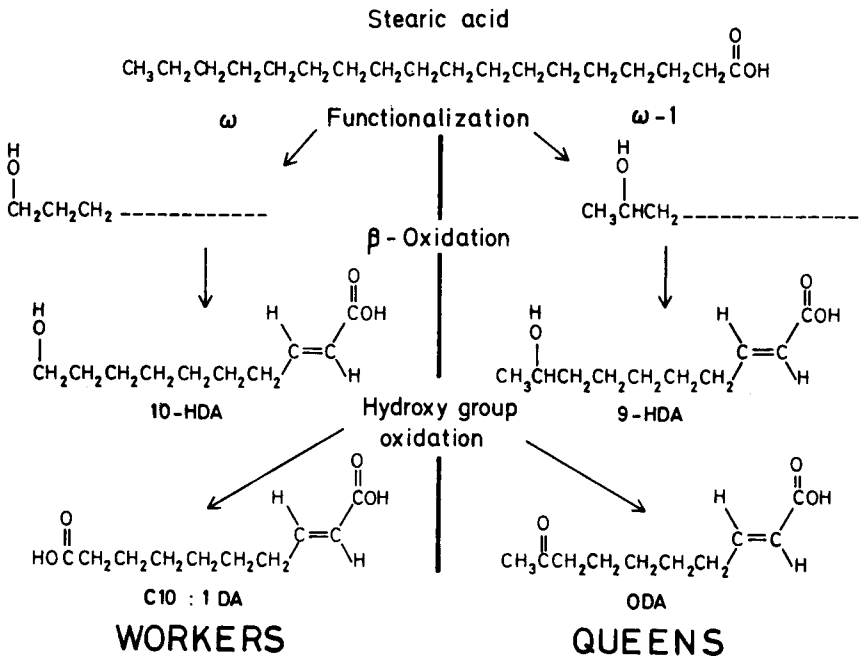


Figure 2. The caste-specific, three-step, bifurcated pathway for the biosynthesis of queen and worker pheromones, as proposed by Plettner et al. (1996).

in the first step, results in the formation of the diacid in the case of workers and the keto acid in the case of queens.

The caste-specific pheromone biosynthetic pathways elucidated by Plettner et al. (1996) permit us to explore yet another and rather different context in which understanding the evolution of chemical communication can tell us much about the evolution of sociality. Of social insect queens and workers, which one is ancestral and which derived? On the one hand, queens in social insect species can be thought of as being comparable to the undifferentiated (into queen or worker) adult insects in their solitary ancestors (or, equivalently, in other extant solitary taxa) and the workers can be thought of as being a new invention of sociality. After all, adults in solitary species are all potentially capable of reproducing, and it is the character of being sterile and merely working to rear another individual's brood that is a novel feature of social insects. On the other hand, workers in social species may be thought of as being comparable to their solitary ancestors or extant solitary counterparts, and the queens can be thought of as an invention of sociality. After all, adults in solitary species are all capable of nest building, foraging and brood rearing and it is the character of inhibiting reproduction of conspecifics and attempting to become the sole reproductive in a group, at the cost of losing foraging and brood rearing abilities altogether if necessary, that is a novel feature of social insects. A reasonable solution to this conundrum is to compromise and think of the solitary insects as queen and worker combined, because each individual is capable of reproduction as well as nest building, foraging and brood care. And this is a largely correct solution because both queens and workers, at least in the advanced social species, are considerably modified and exaggerated in their respective roles compared to solitary insects. Nevertheless, I believe that, if and when possible, we should try to make an objective assessment of whether queens are ancestral and workers are derived or whether it is vice versa. I will argue that the pheromone biosynthetic pathway elucidated by Plettner et al. (1996) provides one such opportunity.

I have recently hypothesized (Gadagkar, 1997a) that, because the pheromone biosynthetic pathway employed by the workers deviates relatively little from the typical lipid metabolism pathway, it might perhaps simply be adopted from there. The diacid they make can be relatively easily channeled into an energy generating role and its degradation products can be profitably fed into the Krebs cycle. On the other hand, I speculate that the pheromone biosynthetic pathway of the queens is quite a deviation from the standard lipid metabolism pathway. In particular, the keto acid is not something one would expect if energy generation is the immediate goal. The expense involved in further breaking down the keto acid makes it a poor candidate to be fed into the Krebs cycle. I therefore speculate that, in the course of making their pheromones, the workers are doing more or less what any solitary insect would do anyway for generating energy from

lipids, and that their pheromone biosynthetic pathway is therefore the more ancestral one. Conversely, queens have considerably modified the ancestral lipid metabolism pathway in order to make a pheromone that has only lately (relatively speaking) become necessary. In order to do so they are prepared to make an end product such as the keto acid which is energetically unwise, but I argue that energy generation is not their motivation here. Surely they have other mechanisms of generating energy even from lipids. And even if their overall efficiency of generating energy from lipids is lower than that of workers, it does not matter that much because it is the foragers, not the queens, that have to fly great distances in search of food. The pheromone biosynthetic pathway of the queens appears therefore to be relatively more derived. One might also argue that the function of the worker pheromone, namely, to act as a preservative and nutrient, is also a more ancestral function, more likely to have been useful in the solitary condition. Conversely, the function of the queen pheromone appears to be more derived as it fulfills a relatively more recent requirement and hence is unlikely to have been of much use in the ancestral solitary condition. Workers thus seem to use an ancestral biochemical pathway to make a product that may also have been required in the ancestral condition. And queens seem to be using a rather derived form of the biochemical pathway to make a product that has a rather derived function. At least in this limited context, workers seem to be ancestral and queens seem to be derived. This one context, important as it is, cannot be thought to have solved our general problem of who came first, the queen or the worker. It would be prudent, even necessary, to be on the look out for more opportunities to classify queens and workers as ancestral or derived. Indeed, a new and highly derived function of the worker pheromone may yet be discovered which may alter our conclusion. Thus, we may well come up with different conclusions each time and only the relative scores for "ancestral" and "derived" that queens and workers accumulate in the long run can help us solve this conundrum in any general sense. But I believe this is a good beginning. We see once again that an understanding of the evolution of chemical communication can lead to important insights into the evolution of sociality itself.

The evolution of caste polymorphism

Yet another striking feature of the social insects, the highly social insects in particular, is the morphological differentiation of queens and workers which may sometimes reach such proportions that, if encountered separately, queens and workers may get classified as different species (Wheeler, 1913). While there is considerable differentiation between honey bee queens and workers, the greatest intra-specific size variations has been recorded in the Asian ant *Pheidologeton diversus* where some workers

weigh 500 times and have a head width 10 times larger compared to other workers (Moffett, 1987). Here the differentiation is not between queens and workers, but rather between the so-called major workers and minor workers. Whether it is between queens and workers or between major and minor workers, these extreme degrees of intra-species, intra-sexual dimorphism require an explanation. The fact that no solitary species seem to match these levels of differentiation suggest that the explanation is linked to the social habit of these insects.

I have recently offered a speculation (Gadagkar, 1994, 1996b, 1997d) which was inspired by the idea of evolution by gene duplication first suggested by Haldane (1932) and Muller (1935) and elaborated and championed by Ohno (1970). The idea is that redundant, duplicate copies of genes can accumulate potentially lethal mutations without killing the organism and can eventually give rise to novel genes coding for novel structures via pathways that would be inaccessible to an individual with a single copy of the gene. I have argued that a very similar consequence will accrue to social insects, although for a somewhat different reason. The evolution of altruistic sterile worker castes in the social insects was considered paradoxical until Hamilton proposed the theory of inclusive fitness (Hamilton, 1964a, b). Today it is common practice to recognize inclusive fitness as having two components, a direct component gained through production of offspring and an indirect component, gained through aiding close genetic relatives. Sterile worker castes are expected to gain fitness exclusively through the indirect component (Wilson, 1971, 1975; Hölldobler and Wilson, 1990), and in no other group is there a comparable level of dependence on the indirect component of inclusive fitness.

I argue that, when some individuals in a species begin to rely on the indirect component of inclusive fitness while others continue to rely on the direct component, as workers and queens in social insects do, different sets of genes in queens and workers will be liberated from previous epistatic constraints. These genes then become free to evolve in new directions. There is no gene duplication here in the conventional sense, but the consequence, namely, liberation from previously existing constraints (due to the action of stabilizing selection) and the opportunity to diversify in different directions (through the action of directional selection), is similar. To put it simply, an individual can evolve into a "super" egg layer if it does not have to simultaneously be a very good forager, or it can evolve into a "super" forager if it does not have to simultaneously be a very good egg layer.

I have speculated that, compared to solitary species, social insects are also in a better position to exploit the evolutionary advantages of conventional gene duplication (Gadagkar, 1997d). I argued in the previous section that the function of the worker pheromone and the biochemical pathway involved in its production are relatively more ancestral, and that the function of the queen pheromone and the biochemical pathway involved in its

production are relatively more derived. If this is true, then it is not difficult to see the tremendous advantage of conventional gene duplication in developing the derived condition from the ancestral one. It seems likely that the enzymes involved in the β oxidation step (see Fig. 2) give rise to specificity for substrates hydroxylated at the ω or $\omega-1$ positions. Imagine that the ancestor of the social insect species had a gene that coded for an enzyme which could deal only with the substrate that was hydroxylated at the ω position. The workers in the descendant social species can continue to use this gene and this enzyme to make worker pheromones which may perhaps have even been made by the ancestor. A duplication of the gene involved can permit the evolution of an alternate enzyme which can handle the substrate hydroxylated at the $\omega-1$ position. We know that such a substrate must already have been available, because both kinds of hydroxylations occur to an equal extent in both queens and workers. The duplicated gene would now be free to evolve in new directions without reduced fitness due to the reduction in the efficiency of energy production through lipid metabolism. Thus, new directional evolution can sometimes give rise to substances with remarkable properties such as the queen pheromone. A similar chance occurrence of such a mutation could hardly have been utilized effectively by a solitary species. Because social insects set aside some individuals for the sole purpose of monopolizing reproduction and inhibiting and controlling all others, they are in a special position to exploit such a consequence of conventional gene duplication and evolve in directions that are not open to solitary species. Once again we see an intimate link between possible mechanisms of evolution of chemical communication and those of the evolution of sociality.

Conclusion

We have discussed six hypotheses concerning the evolution of chemical communication between the honey bee queen and her workers and considered their implications for the evolution of sociality (Tab. 1). Today we are not quite in a position to unambiguously ascertain the correctness or otherwise of any of these hypotheses. However, these hypotheses are testable and are therefore expected to lead eventually to a better understanding of the evolution of chemical communication and hence to a better understanding of the evolution of sociality. But if this is the situation today with respect to honey bee whose queen pheromone is the best studied one, imagine the situation with respect to other species of social insects. If details concerning the evolution of chemical communication such as exemplified by the hypotheses considered here vary between honey bees and other social insects, our conclusions regarding the evolution of insect sociality will necessarily have to be revised as new information becomes available from different species. The evolution of social life in insects and

Table 1. Hypotheses concerning the evolution of chemical communication between honey bee queens and workers and their implication for our understanding of the evolution of sociality. Hypotheses 1 and 2 based on Keller and Nonacs (1993), hypothesis 3 based on Zahavi and Zahavi (1997) and hypotheses 4–6 based on Gadagkar (1996, 1997d,e).

| <i>Hypothesis</i> (concerning the evolution of chemical communication) | <i>Implication</i> (for the evolution of sociality) |
|---|---|
| 1. Queen pheromone is a weapon used by the queens to control the workers and force them to act against their best interests | Social insect colonies are evolutionary unstable with scope for mutations that make the workers revolt against the hegemony of the queen. |
| 2. Queen pheromone is a signal used by the workers to do what maximizes their (and perhaps the queen's) inclusive fitness. | Social insect colonies are evolutionary stable associations of queens and workers that maximize their own and each others inclusive fitness. |
| 3. Queen pheromone is a poisonous handicap carrying of which gives an individual (queen or worker) prestige which translates into opportunities for reproduction. | Social insect colonies (including the apparent altruism of workers) are moulded by individual selection where each individual, queen or worker, is doing the best it can under the circumstances. |
| 4. Queen pheromone biosynthetic pathway is derived by a modification of the worker pheromone biosynthetic pathway that already existed in the solitary ancestral species. | In social evolution, workers are ancestral and queens are derived, suggesting that groups of worker-like individuals came together and queens evolved later as a consequence of social life. |
| 5. Worker pheromone biosynthetic pathway is derived by a modification of the queen pheromone biosynthetic pathway that already existed in the ancestral solitary species. | In social evolution, queens are ancestral and workers are derived suggesting that groups of queen-like individuals came together and workers evolved later as a consequence of social life. |
| 6. The derived pheromone biosynthetic pathway (be it the queen's or the workers') is made possible by a gene duplication event at the locus coding for one of the enzymes of the ancestral pathway. | Social insects are in a unique position to utilize the consequences of gene duplication because in the same species queens and workers follow different developmental pathways and require different biochemical pathways to be active. |

especially the evolution of altruism on the part of workers remains a major unsolved problem although it has received much theoretical and empirical attention. Perhaps we have reached something of a dead end because of a possible narrow approach to the problem. The ideas discussed in this chapter suggest that a new spurt of progress may be achieved by temporarily turning our attention away from the explicit consideration of the evolution of altruism and focusing, instead, on other aspects of sociality – the evolution of chemical communication being just one example.

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