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The role of queen pheromones in social insects: queen control or queen signal?

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Abstract. Queens and workers in social insect colonies can differ in reproductive goals such as colony-level sex allocation and production of males by workers. That the presence of queen(s) often seems to affect worker behaviour in situations of potential conflict has given rise to the idea of queen control over reproduction. In small colonies queen control is possible via direct aggression against workers, but in large colonies queens cannot be effectively aggressive towards all the workers. This, plus evidence that queen-produced chemicals affect worker behaviour, has led to the conclusion that physical intimidation has been replaced by pheromonal queen control, whereby queen(s) chemically manipulate workers into behaving in ways that increase the queen's fitness at the worker's expense. It is argued in this paper, however, that pheromonal queen control has never conclusively been demonstrated and is evolutionarily difficult to justify. Proposed examples of pheromonal control are more likely to be honest signals, with workers' responses increasing their own inclusive fitness. A series of experimental and field studies in which positive results would give prima facie evidence for pheromonal queen control is suggested. Finally, three terms are defined: (1) pheromonal queen control for workers or subordinate queens being chemically manipulated into acting against their own best interests; (2) pheromonal queen signal for situations where workers or subordinate queens react to queen pheromones in ways that increase their, and possibly the queens', inclusive fitness; and (3) pheromonal queen effect where changes in the workers' or subordinate queens' behaviour have an unknown consequence on their inclusive fitness.

Social insect colonies typically contain two castes: queens, which lay most of the eggs, and workers, which have reduced fertility and undertake most of the tasks required to maintain the colony. This reproductive division of labour has important consequences in that queens and workers frequently have different reproductive goals in matters such as sex allocation, the number of reproductively active queens within a colony, and whether workers can lay viable eggs (Trivers & Hare 1976; Nonacs 1986, 1988; Bourke 1988; Boomsma, in press).

There are examples in many species of different reproductive strategies in colonies where queens are absent compared with colonies with queens. For example, in queenless colonies, worker reproduction is much more frequent and both worker-to-sexual and female-to-male production ratios decrease (Brian 1983; Bourke 1988; Herbers 1990; Hölldobler & Wilson 1990).

The theoretical expectation of queen–worker conflict and observed effects of removing queens has led to the concept of 'queen control', which can be defined as workers or subordinate queens being manipulated by a dominant queen into pursuing actions that are contrary to their inclusive fitness (or conversely, that workers can only do what is best for themselves when queens are dead or absent). In eusocial species with small colony sizes this control can be through physical intimidation leading to dominance hierarchies between the queen and all her subordinates or workers. However, when colonies are composed of thousands to millions of individuals, queen control by physical domination alone is unlikely, if not impossible. In these colonies, manipulation of workers has been proposed to occur through 'pheromonal queen control' whereby chemicals exuded by the queen(s) replace physical intimidation in forcing workers to behave in ways that increase queen fitness

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(reviewed in Wilson 1971; Watson et al. 1985 (termites); several chapters in Ross & Matthews 1991 (wasps); Michener 1974 (bees); Hölldobler & Wilson 1990 (ants); see also Fletcher & Ross 1985; Hölldobler & Bartz 1985).

The hypothesis of pheromonal queen control has recently been challenged in relation to worker reproduction in the honey bee, *Apis mellifera* (Seeley 1985; Woyciechowski & Lomnicki 1987; Ratnieks 1988; see below). However, the term queen control continues to be broadly used, often without sufficient distinction as to whether or not queens are, in an ultimate sense, manipulating other colony members to gain fitness at their expense.

In this paper we argue that pheromonal queen control, defined as manipulation and control through chemical production alone, has never been conclusively shown to exist and is unlikely to have evolved. Furthermore, existing examples of pheromonal inhibition of reproduction have not been shown to be contrary to the reproductive interests of the target organisms. True queen control, we argue, is likely to be found only when direct, physical aggression against all subordinates is possible with pheromones serving as honest signals rather than as controlling substances.

EVOLUTION OF PHEROMONAL QUEEN CONTROL

There are two possible evolutionary pathways through which effective pheromonal queen control might have arisen.

(1) Queens produce a chemical which 'must be obeyed'. In other words, queens hold a substantial advantage in a chemical arms race against subordinates (see West-Eberhard 1981). However, there are several reasons why this is unlikely. If workers or other queens have their fitness significantly reduced, there would be strong selection to escape control by building up tolerance or immunity to the pheromone. For queens to retain strong control they would therefore have (i) continually to produce new (or mixtures of) compounds to stay one step ahead of the workers, and/or (ii) to invest more and more resources in producing larger quantities of the pheromone as effective dosage levels rise. Both of these solutions would eventually lose cost-effectiveness: i.e. queens would probably gain more overall fitness by allowing others to win in some respects (e.g. sex ratios and worker reproduction) rather than indulge in an escalating arms race that would eventually decrease overall colony productivity (see Ratnieks & Reeve 1992, for a discussion of how queen–worker conflicts may be diminished if they result in decreased colony productivity). Furthermore, pheromones are known to be distributed to all colony members so that a queen attacking others chemically is also likely to be affecting herself. This is particularly true in the case where pheromones have been hypothesized to regulate reproductive roles of nestmate queens. A queen producing a chemical aimed at decreasing other queens' fecundity could decrease her own reproductive output. Only if the response threshold of queens correlated with their fecundity, such that the effectiveness of the pheromone diminishes with fecundity, might it benefit fecund queens to produce inhibitory chemicals. The available evidence suggests that this is not the case. In the ant *Solenopsis invicta*, queen-produced pheromones reduce reproductive output in all queens, independent of fecundity (Vargo 1992).

The concept of intraspecific pheromonal control of other individuals seems virtually unique to eusocial insects. Although analogues to eusociality outside of insects are rare, many species do form social groups and a preponderance of species exhibit some social behaviour if only in reproductive contexts (i.e. mating and parental care). Certainly there must be many contexts in which pheromonal control of the behaviour or reproductive output of other individuals could increase the sender's fitness. The paucity of evidence for chemical control in other species strongly suggests that such control is not evolutionarily stable.

(2) Queens produce a dishonest signal that fools other colony members into performing actions that favour the queens. A prime example would be in species that have only one queen per colony (monogynous), for those queens to convince their workers that they are multiply mated (polyandrous). The benefits for a singly mated queen of fooling workers about her mating status are twofold in social Hymenoptera. First, such a queen can produce all the colony's males if her workers behave as if she were multiply mated. Workers are more related to their own sons ($r = 0{\cdot}5$) and their full-sister's sons (0·375) than they are to their brothers (0·25). However, workers are more closely related to brothers than they are to their half-sister's sons (0·125). If a queen has mated with more than two unrelated males, workers can increase their

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fitness by preventing others (who are mostly half-sisters) from producing males at the expense of their mother's production of males (Starr 1984; Woyciechowski & Lomnicki 1987; Ratnieks 1988). Second, a perception of multiple mating would reduce the workers' proclivity for female-biased sex ratios in monogynous species (Trivers & Hare 1976). If the population-wide sex ratio is female biased, queens should always favour male offspring. Workers, if they perceive themselves to be equally related to the average male and female sexual due to multiple mating, will have optima similar to the queen and will therefore also favour the production of males (Boomsma & Grafen 1990, 1991). However, because queens may always benefit by indicating a higher number of matings it is unlikely that workers would rely on a signalling system derived from the queens themselves (all queens would signal they are multiply mated!). Instead workers could use honest and readily available information from the odour variation due to genetic causes of their sisters to assess queen mating frequency (Ratnieks 1990).

In a general treatment of the problem, Dawkins & Guilford (1991) showed that an honest signalling system can be invaded by deception when correct identification of a signal is costly or time-consuming. In social insects this could drive sexual deception through which queens may maintain control of parentage of males, in opposition to workers interests, by hiding the sex of their offspring during the early stages of their development (Nonacs & Carlin 1990; Nonacs 1992). In monogynous species with singly mated queens, workers would increase their inclusive fitness by replacing brothers (the queen's sons) with sons and nephews (their own or their sisters' offspring). However, such replacement is never favoured if workers cannot reliably tell the sex of larvae before development is one-third complete (i.e. if highly related female larvae are mistakenly destroyed along with the males: see Nonacs 1992). However, although sexual deception manipulates workers, it cannot be regarded as pheromonal queen control because the males should be willing collaborators in the deception and, fundamentally, the success of the deception is likely to be much more dependent on the males' ability to mimic their sisters through early development than on any chemical produced by the queen. Nevertheless, it is illustrative to see why dishonesty about sex of larvae works and why dishonesty about queen mating number does not. Although both males and singly mated queens should always lie about their respective sex or mating number workers need not 'trust' queen-produced signals about mating number. As argued above, they can use their own reliable, genetic odour diversity instead. However, the sex of larvae can be determined only through examining the larvae themselves, because independent indicators of sex do not exist. With workers encountering mostly honest signals of females signalling femaleness along with a relatively few deceptive males (males are always relatively rare because most larvae are female workers), dishonesty can be an invading strategy (Dawkins & Guilford 1991).

In sum, dishonesty can exist in social insect colonies as with sexual deception, but true pheromonal queen control though dishonest signals is unlikely to be evolutionarily stable because alternative reliable, worker-produced signals will negate the dishonest system. Unreliable signalling systems will not be preferred to reliable systems (see Dawkins & Guilford 1991) and, therefore, the existence of queen-produced pheromones suggests that they are honest messages of queen intent or presence.

CONTROL OR SIGNAL?

Queen control, mediated through pheromones, has been suggested as a cause for the following four colony characteristics. We propose, however, that there are equally valid alternative explanations for all the phenomena.

Inhibition of Worker Reproduction

In many species workers have egg-laying potential, but do not lay viable eggs in the presence of queen pheromone (e.g. Passera 1984; Bourke 1988; Hölldobler & Wilson 1990). In eusocial species with small colony sizes, pheromones may be honest signals of queen fighting ability and fecundity (West-Eberhard 1977) and they may suppress worker reproduction, not because of their own intrinsic power, but because of the information that they convey about queen resource-holding potential. It has indeed been shown that subordinates and workers may suffer strong attacks from the queens if they try to reproduce (West-Eberhard 1977). True pheromonal queen control, as we would define it, would not have to be reinforced through physical aggression.

In species with large colonies, pheromones may act as a cue, signalling queen presence. In an ultimate sense, queen presence may select for workers inhibiting their own reproduction, which is proximately manifested by their reaction to pheromones. There are three possible explanations of why workers would not be favoured to reproduce in the presence of fertile queens. (1) If workers are on average less related to nestmate workers' sons than to sons of the queen(s) because of polyandry, workers increase their fitness by preventing other workers from laying male eggs (Starr 1984; Woyciechowski & Lomnicki 1987; Ratnieks 1988; see above). Ratnieks & Visscher (1989) found that in the highly polyandrous honey bee, workers destroy almost all worker-laid eggs when a queen is present in the colony. (2) If colony productivity is significantly reduced as a result of worker reproduction, because workers are less eager or able to undertake essential tasks, such as foraging or defence of the colony, workers may refrain from reproducing (Cole 1986; Ratnieks 1988; Ratnieks & Reeve 1992). (3) If sexual deception keeps workers from detecting the sex of the queen's offspring early in their development, workers gain no advantage by replacing them with their own male eggs (see above and Nonacs 1992). Sexual deception is supported in the ant *Camponotus floridanus*, where workers can detect the sex of the brood at the pupal stage, but not early in development in the egg and larval stages (Nonacs & Carlin 1990).

Thus, rather than being chemically manipulated, workers may use queen pheromones as signals to detect her presence, and ultimately refrain or prevent other workers from reproducing in the colony because it increases their fitness.

Inhibition of Subordinate Queen Reproduction

There is tremendous variation from equality of reproductive output to complete domination by a single queen in polygynous colonies of eusocial insects (Keller & Vargo, in press). When several queens contribute to the colony's reproduction, there is an inverse relationship between queen number and the fertility of individual queens (e.g. Michener 1964; Roisin & Pasteels 1985; Keller 1988; Keller & Passera 1989a; Vargo & Fletcher 1989). It has been suggested that dominant queens entirely or partially inhibit the reproductive output of subordinate queens (Vargo & Fletcher 1989; Heinze & Smith 1990). In *S. invicta*, corpses of dead queens effectively inhibit the fecundity of functional queens, suggesting that queen-produced pheromones do suppress egg production in functional queens (Vargo 1992). There are two possible mechanisms which may account for this pheromonal effect: the pheromone may act directly on the physiology of queens; or workers may use the pheromonal signal to regulate queen reproductive output. As mentioned before, the first mechanism seems unlikely since a queen producing a pheromone aimed at decreasing other queens' fecundity is also likely to inhibit her own reproduction as well. Alternatively, workers could use the information derived from pheromone production by queens to regulate the queens' reproductive output and increase colony reproductive efficiency. Depending on factors such as food availability and worker number there is a maximum number of brood that can be cared for. Colony efficiency is maximized when egg production by queens is matched to the number of brood the colony can rear. Because, in *S. invicta*, colony growth is independent of the number of queens in the colony (Vargo & Fletcher 1989), maintaining high colony efficiency requires that per queen fecundity decreases as queen numbers increase. Worker regulation of queen fecundity can be based on the amount of pheromone produced in *S. invicta*, because the fecundity of queens correlates with pheromone production (Fletcher & Blum 1983; Fletcher 1987). Thus, if workers perceive higher than optimal pheromonal levels in the colony (i.e. higher than optimal egg production) they can reduce queen fecundity by feeding them less or behaving aggressively towards the most fecund queens. The latter response is suggested in polygynous colonies of *S. invicta*, where workers behave aggressively towards foreign queens with high fecundities, but readily accept queens with low fecundities (L. Keller, unpublished data).

In some ant species several queens co-exist in the same nest but only one is reproductively active (functional monogyny; Buschinger 1968; Heinze, in press). The dominance hierarchy is set up by aggressive interactions among queens occurring at the beginning of the reproductive season (Heinze & Smith 1990). This monopoly over reproduction is maintained later in the year without physical aggression, but this need not imply chemical suppression of the subordinates. Rather, reproductive status (and, eventually, associated differential pheromone production) might act as signals of the

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Inhibition of Dealation and Reproduction by Virgin Queens

Fletcher & Blum (1981) showed that virgin females of the monogynous form of the ant *S. invicta* readily shed their wings (dealate) and start producing male eggs if the mother queen is removed. On the basis of this and other experiments showing that corpses of dead queens also prevent dealation and reproduction of virgin females, they concluded that the inhibitory effect results from pheromonal queen control. However, when virgin queens are reared in queenless fragments of the mother colony, they dealate and start producing male eggs without negative consequences, but are immediately attacked and killed by workers upon reintroduction to their mother colony (L. Keller & K. G. Ross, unpublished data). With a queen present in the colony, the workers benefit from preventing virgin females from laying male eggs for the same reasons invoked for worker reproduction (see above). Furthermore, allowing virgins to dealate and reproduce decreases the number of queens that disperse to start new colonies. However, under queenless conditions it is to the workers' benefit to let virgin queens reproduce because *S. invicta* workers have vestigial ovaries and are totally sterile. Thus, only virgin queens have the potential to reproduce in queenless colonies. Under this scenario, the queen pheromone acts as a signal telling workers whether to allow virgin queens to reproduce, and informing virgin queens whether they will be able to reproduce without being killed by workers.

Inhibition of Female Brood Differentiation into Sexuals

In many species, the presence of the queen prevents the production of sexuals, such that when the queen is present the production of sexuals is restricted to large colonies (Wilson 1971; Vargo & Fletcher 1986; Hölldobler & Wilson 1990; Vargo & Passera 1991). Some have, therefore, concluded that queens prevent the production of sexuals, but that they lose 'control' when the colony gets too big (e.g. Brian 1983, page 205; Fletcher & Ross 1985). This conclusion assumes that it is always to the workers' advantage that larvae become sexuals. This is certainly true if the colony has become queenless and has no long-term future, but is not always true if the queen is alive. Larvae that become workers in colonies with queens will contribute towards colony defence, brood care and food collection. All of these contributions will increase colony survival and can result in greater lifetime production of sexuals. Furthermore, in species that reproduce by colony fission, both workers and sexuals need to be produced for the colony to reproduce (Keller 1991). Production of sexuals by only large colonies can be explained because, the larger the colony is, the lower will be the benefit of each new additional worker in terms of increasing colony survival. Once the colony has reached a given size, all members of the colony should favour a strategy where part of the colony resource is devoted to the production of sexuals. Thus, the production of sexuals mostly in large colonies follows simply from ergonomic efficiency rather than pheromonal queen control.

EVIDENCE FOR PHEROMONAL QUEEN CONTROL

We suggest that the four following experiments or observations would demonstrate the existence of pheromonal queen control. In each case, positive results would be difficult to explain in any other manner than by pheromonal control hence supporting the queen control hypothesis. Negative results cannot conclusively reject pheromonal queen control, but would seriously weaken the hypothesis.

(1) All other things being equal, inhibitory effects of the queen on worker reproduction are not positively correlated with the queen's egg-laying ability. If the inhibitory effects are positively correlated with the queen's egg-laying ability, the queen-produced pheromones can be interpreted as being honest signals of the queen's reproductive abilities that workers use to their advantage (e.g. if queens

get too old to reproduce, workers should not refrain from reproducing). Similarly, the attention queens get in polygynous colonies should be linked to their reproductive abilities; in an honest, non-queen-controlled situation, queens with low fecundity should not be able to outcompete more fecund queens for worker attention and feeding.

(2) Queens that produce only male eggs (either permanently or seasonally) always have the same inhibitory effects on worker reproduction as female-producing queens. Workers can favour rearing males produced by their mother queen, rather than their own sons or those of worker sisters, if replacing the queen's eggs has a cost (i.e. destroying female eggs produced by the queen, see above and Nonacs 1992). However, if the queen produces only male eggs, there is no risk of destroying female eggs and workers should be more likely to reproduce themselves, and even possibly eliminate a queen that does not produce female eggs (as may occur if she runs out of sperm). However, sexual deception would predict a lag time in workers recognizing that a queen has switched from the production of both sexes to only male production. This lag time depends on the stage in preimaginal ontogeny at which the sexes can first be unequivocally distinguished by workers.

(3) Worker reproduction or ovariole development decreases as fecund queen number increases in a polygynous colony (i.e. more fertile queen = higher pheromonal production = greater control of worker reproduction). In contrast, if the pheromone is only a signal, there is no reason why worker reproduction should decrease with increasing queen number. Rather, it should probably increase because lower colony relatedness would favour more selfishness in the worker's behaviour (Nonacs 1992).

(4) In species in which, owing to their social systems, queens and workers have demonstrably different optimal reproductive strategies, population values reflect the queens' optima. One type of test case would be species in which colonies are monogynous with singly mated queens and obligately sterile workers (e.g. *S. invicta*). As shown by Trivers & Hare (1976) queens will always favour a 1:1 sex ratio while their workers will favour a 3:1 female-biased ratio and no single solution can maximize the inclusive fitness of both parties simultaneously. Unfortunately, empirical estimation of investment sex ratios on the population level is hard, mainly because of the difficulty of estimating the real female-to-male cost ratio (Passera & Keller 1987; Boomsma 1989; Keller & Passera 1989b). A second test case would be colonies with very low relatedness due to high levels of polygyny and polyandry. Kin selection predicts that workers should produce sons at the expense of males produced by the queen (Nonacs 1992), whereas pheromonal queen control predicts that the high number of queens would result in high pheromone levels and thus suppression of worker laying.

CONCLUSIONS

In summary, we argue that significant queen control over colony reproduction, when considered in an ultimate, evolutionary sense, is possible only where physical intimidation of all or most of the colony members can occur. Control, based solely on pheromones with manipulating capacities, is difficult to explain evolutionarily. The existence of proximate effects due to queen-produced chemicals does not demonstrate control and the leading examples in the literature can be interpreted as increasing not only the queens' fitness, but also that of the other colony members. Future studies must take great care in clearly identifying and eliminating alternative explanations because distinguishing between manipulative control and informative signal is crucial with regard to the outcome of conflicts of interest between members of complex societies. A system of nomenclature should therefore take into account the effect of the pheromone on the fitness of the target organism. To this end we propose the use of the following terms: 'pheromonal queen control' for situations where workers or subordinate queens are chemically manipulated by queen(s) into pursuing actions that are contrary to their inclusive fitness; 'pheromonal queen signal' for situations where workers or subordinate queens react to queen pheromones in ways that increase their (and possibly the queens') inclusive fitness; and 'pheromonal queen effect' where changes in the worker or subordinate queens' behaviour have an unknown consequence on their inclusive fitness.

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