The evolution of honest queen pheromones in insect societies

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Social insect workers are often capable of reproduction, but will not do so in the presence of a fertile queen. In large societies, queens are expected to produce a pheromone that honestly signals her dominance and/or fertility, to which workers respond by suppressing the development of their ovaries and by preventing other workers from reproducing (worker policing). However, what maintains the honesty of such queen pheromones is still under discussion. The explanation that an honest queen signal evolves simply because it serves the interest of all colony members does not seem to hold, since it is undermined by the fitness benefits of direct reproduction of workers at the individual level. A better explanation may be found in the idea that queen pheromones are difficult to produce for subordinate individuals, either because policing workers attack them, or because queen pheromones are intrinsically costly chemicals. Here, I discuss some of the arguments for and against these hypotheses and the evolutionary scenarios that each would lead to.

Key words: social insects, queen pheromone, honest signals, division of labor, worker policing

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Introduction

Societies of ants, wasps, bees and termites are characterized by a reproductive division of labor. One or few individuals reproduce [generally the queen(s)], whereas most of the workers take care of other tasks.[1-3] The high fitness cost that workers pay by not reproducing themselves can be evolutionarily explained by inclusive fitness theory: by directing altruistic behavior to highly related individuals, the workers' indirect fitness benefits can outweigh the direct fitness costs.[4] However, workers of many social insect species are not sterile and start reproducing (these unfertilized eggs will generally develop into males) rapidly if the queen dies or is removed, which has classically led to the view that subordinate workers are manipulated into altruistic behavior by their dominant queen ('queen control').[5,6] In small Hymenopteran societies, like those of *Polistes* wasps or Halictid bees, queen control could be achieved by overt aggression towards subordinate individuals and destruction of their brood, which has been referred to as 'queen policing'[7] or 'physical intimidation'.[8] In larger colonies, however, like those of honey bees or most ant species, physical queen control appears to be largely displaced by queen pheromones to suppress ovary development of workers,[9] likely because it is virtually impossible to aggressively intimidate all workers. However, true pheromonal queen control, i.e., queen pheromones that exert direct ovary-inhibiting or manipulating features, is arguably evolutionary unstable, since evading the effects of these pheromones is favored if remaining sterile is against the workers' interests.[8] An alternative hypothesis is that the queen pheromone is an honest signal of her quality and/or her presence. Workers benefit from responding to this signal, given that it reliably reflects the queen's egg-laying potential and reproductive workers typically reduce the inclusive fitness of the worker collective.[8] In support of the queen signal hypothesis, queen pheromones appear to vary positively with egg-laying potential across social insect species.[10] In addition, worker reproduction is indeed expected to reduce the workers' inclusive fitness on relatedness grounds and/or colony efficiency grounds,[7] so that in the presence of a fully fertile queen, workers counteract each other's reproduction by destroying worker-laid eggs or aggressive behavior towards reproductive workers. This so-called worker policing has been shown in many species of social Hymenoptera,[11] in support of the honest queen signal hypothesis.

What Maintains the Honesty of a Queen Signal?

Honest signals are hypothesized to remain evolutionary stable when they comprise either an index (a signal that simply cannot be faked, because it is intrinsically linked to the property it is providing information about), a handicap (a signal of which the cost of production or maintenance assures that individuals of low quality are unable to produce such a signal[12]) or when they provide mutual benefit to all parties involved.[13] Can the evolution of honest queen pheromones be explained by mere mutual benefit? This hypothesis fits well with a traditional group-selection point of view[14] and is subject to the same criticism, namely that individual selection is faster and likely a stronger evolutionary force than selection at the group level.[15] It may benefit both queens and the worker collective to respectively produce and respond to a queen pheromone, but, all else being equal, a mutation that causes workers not to respond can easily invade in the population, for it will increase the fitness of individuals carrying this selfish mutation. Therefore, this argues against the mutual benefit hypothesis for the maintenance of honest queen pheromones.

The presence of policing workers in insect societies also argues against the mutual benefit hypothesis, having evolved to counteract selfish reproductive workers. In addition, it shows that selfish workers, in order to reproduce successfully, would have to escape detection by these policing workers. An hypothesis as to why workers would not be able to escape detection was recently voiced by Smith and co-authors,[16] namely that the production of signals on eggs necessary to let them be accepted by other workers are intrinsically linked to the expression of these signals on the cuticle of the egg-layer (i.e., an index hypothesis). The expression of these signals on the worker cuticle would lead to aggressive policing behavior by other workers, so that worker reproduction is counteracted. This hypothesis fits well with the observation that in a number of ant species queen-cuticle-specific hydrocarbons are also found on queen-laid eggs, but not on worker-laid eggs,[17-20] and with the observation that the expression of queen-specific substances vary with ovarian activity.[16,18,21-25]

But why were certain substances co-opted as queen pheromones in the first place? For this question, we should probably look back at what happened when the dominant individuals in insect societies first moved from aggression to pheromones, where queen pheromones may have signaled fighting ability or fertility.[26] The evolutionary scenario under the index hypothesis could be that the individual with most fighting ability becomes the dominant, and therefore the egg-laying individual with developed ovaries. Ovary development and egg production could, for as-yet unclear physiological reasons, be associated with the by-production of a set of chemical cues, that through ritualisation could become a dominance signal (i.e., a queen pheromone as an index of egg production). Any subordinate individual producing this set of cues is attacked, which makes the signal therefore difficult to produce and kept honest.

Alternatively, a handicap hypothesis could provide a scenario where specific molecules are utilized that are themselves physiologically expensive to produce, and there is thus a trade-off between fighting ability and pheromone production. Dominant individuals start signaling that despite the production of these costly chemicals, they are still able to behaviorally dominate the colony and produce eggs. Subordinate individuals start responding to this signal and avoid aggression towards the dominant, since they are unlikely to win and none of the parties benefits from escalated fights. This costly signal, which will subsequently evolve into a queen pheromone, can also be deposited on the eggs to communicate that these are eggs laid by the dominant individual. This handicap hypothesis fits better with the way in which the queen mandibular pheromone (QMP) of *Apis mellifera* is regulated, since its components are not found on queen-laid eggs,[27] nor do they vary strongly with ovary development or egg-production.[28]

Among ant species, several queen-specific compounds in the cuticular hydrocarbon profiles have been found. There seems to be a general trend in using alkenes and shifts in the average chain length of the hydrocarbon profile,[29] and a high frequency of the use of 3-methyl and 3,y-dimethyl alkanes. Do these queen pheromone strategies represent the usage of costly physiological pathways to signal dominance and egg-laying potential? Or do these compounds represent coincidental by-products of ovary development that have been co-opted in signaling fertility? Future research should verify if compounds indeed induce or maintain suppression of worker ovary development, try to disentangle dominance and fertility as causes for the production of these queen pheromones, and test whether queen pheromone molecules are intrinsically more costly to produce than those characterising less fertile individuals. Hopefully this will elucidate the proximate causes in the evolution of reproductive division of labor in insect societies, which contributes largely to their ecological success and communicative sophistication.

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