

Queen pheromones

The chemical crown governing insect social life

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Group-living species produce signals that alter the behavior and even the physiology of their social partners. Social insects possess especially sophisticated chemical communication systems that govern every aspect of colony life, including the defining feature of eusociality: reproductive division of labor. Current evidence hints at the central importance of queen pheromones, but progress has been hindered by the fact that such pheromones have only been isolated in honeybees. In a pair of papers on the ant *Lasius niger*, we identified and investigated a queen pheromone regulating worker sterility. The cuticular hydrocarbon 3-methylhentriacontane (3-MeC₃₁) is correlated with queen maturity and fecundity and workers are also more likely to execute surplus queens that have low amounts of this chemical. Experiments with synthetic 3-MeC₃₁ found that it inhibits ovarian development in queenless workers and lowers worker aggression towards objects coated with it. Production of 3-MeC₃₁ by queens was depressed by an experimental immune challenge, and the same chemical was abundant on queen-laid eggs, suggesting that the workers' responses to the queen are conditional on her health and fecundity. Together with other studies, these results indicate that queen pheromones are honest signals of quality that simultaneously regulate multiple social behaviors.

Parsimonious Regulation of Colony Life by Queen Pheromones

In combination with previous results, our new data^{1,2} suggest that queen pheromones can simultaneously regulate multiple

aspects of reproductive division of labor and other colony-level processes (Fig. 1). We found that the cuticular hydrocarbon 3-MeC₃₁ is involved in signalling queen fertility, maturity and condition,^{1,2} regulating worker reproduction² and preventing worker aggression towards objects bearing the pheromone.² Several other functions are more tentatively supported. Our results on the execution of supernumerary queens in founding associations are consistent with selective worker aggression towards the queen(s) with the least 3-MeC₃₁.¹ Workers that cannot directly identify their mother are predicted to attack queens that have produced the fewest workers, maximizing the chance that they are killing an unrelated queen,^{1,3} and 3-MeC₃₁ is strongly correlated with queen productivity.

Queen-like chemicals have also been implicated in the aggressive response to non-preferred reproductives, such as fertile workers and subordinate reproductives, in many other species of ants⁴ (especially queenless ants⁵), wasps⁶ and bees.⁷ Our results and those of Moore and Liebig⁸ imply that queen-like hydrocarbons depress worker aggression, which is seemingly incongruous with reports of these same chemicals eliciting aggression in certain contexts, e.g., when expressed by fertile workers or subordinates.^{4,5} This disparity suggests either (A) queen pheromone has a dose-dependent effect on aggression, i.e., weak sources of pheromone attract aggression while strong sources repel it or (B) that there are multiple cues involved in the aggressive response, such that queen pheromone excites or inhibits aggression in combination with other stimuli. The dose-dependent hypothesis seems more parsimonious, although explicit tests are needed.

Key words: social insect, queen pheromone, fertility signal, cuticular hydrocarbon, social physiology, primer pheromone

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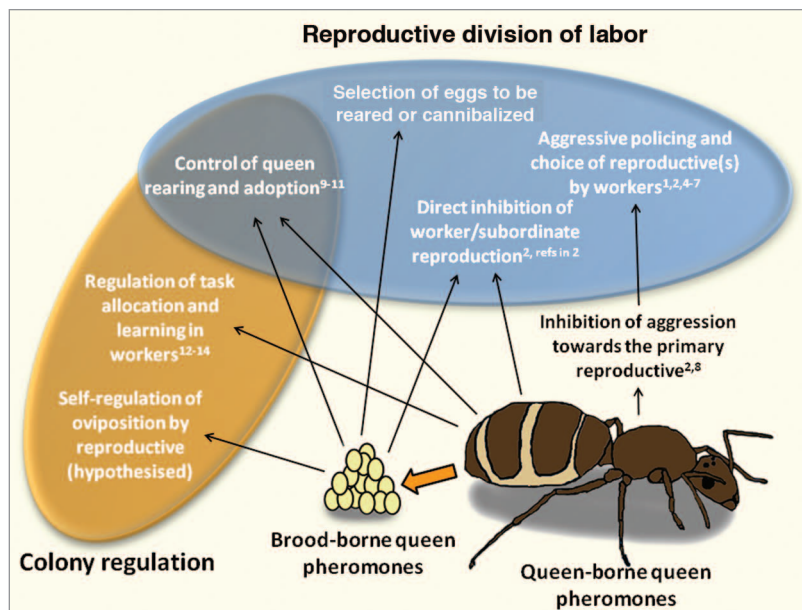


Figure 1. Known and hypothesized functions of queen pheromones produced by queens (or other reproductive individuals) and carried on their brood. The numbers give a non-exhaustive list of studies providing evidence consistent with each function.

I also propose that queens pheromones may be used by queens to regulate their own reproductive output with respect to external cues, e.g., the number and developmental stage of brood and the presence of other queens competing to be the sole reproductive.¹ There is indirect evidence of this in *L. niger*: 3-MeC₃₁ is present on queens, eggs and cocoons,^{1,2} and queens reduce their reproductive output when additional queens and brood are present.¹

Even more queen pheromone functions have been described in other taxa. Queen adoption,⁹ supersedure¹⁰ and replacement^{10,11} behavior in ants and honeybees is thought to be regulated by queen pheromones, and in honeybees there is extensive evidence that worker task allocation,¹² brain development¹³ and learning¹⁴ is influenced by queen pheromone exposure. Queen pheromones on the surface of eggs are likely to allow discrimination and differential rearing of eggs from different colony members, particularly queens and workers,^{15,16} but perhaps also from different queens.¹⁶

Perspectives for Future Research

There is now near-unanimous support for the hypothesis that social insect queen pheromones are “honest signals” of

fertility or condition, and that the worker response is not counter to their own fitness interests.^{1,2,17-20} I therefore suggest that researchers should focus on the ultimate explanation for this honesty. There are 3 principal reasons why signals should be honest:^{18,21} (1) dishonest signalling is not selected, (2) the signal is a costly “handicap”, such that only high-quality individuals benefit from investing heavily in signalling and (3) the signal is an unfakeable “index” that is inextricably linked to the trait it is signalling. As argued elsewhere,¹⁸ hypothesis 1 is unlikely to be applicable to all social insects, including derived lineages where reproductive conflict is constrained.²² For example, in *L. niger*, we expect that queens in multi-queen colonies would benefit from producing dishonestly high amounts of 3-MeC₃₁ to avoid execution by workers. At present, almost all data on putative queen pheromones appear to be equally consistent with the handicap and index hypotheses. In *L. niger*, our immune challenge might have depressed reproductive physiology causing a corresponding drop in pheromone production (index) or reduced condition such that pheromone production was no longer possible (handicap).² Intriguingly, treatment with juvenile hormone reduced reproductive activity

while slightly augmenting pheromone production in honeybee workers²³ (which appears to falsify the index hypothesis); however, in a comparable experiment in ants both reproduction and putative queen pheromones were suppressed by juvenile hormone.²⁴ Determining the underlying genetic architecture, biochemistry and/or fitness costs of pheromone production may be required to definitively discriminate between these hypotheses.

Our study² shows how queen primer pheromones may be unambiguously identified, and we believe that it will be fruitful to isolate more in additional taxa. This will allow numerous novel questions to be addressed, e.g., how fast do queen pheromones evolve, are they predominantly single- or multi-component blends, and have similar pheromones evolved independently in phylogenetically-distant taxa? Answering these questions will provide insight into social evolution as a whole. For example, fast-evolving and multi-component signals imply coevolution and possibly conflict.^{17,21} Convergent evolution of homologous queen pheromones would suggest that certain chemicals are particularly suited to the job: they might be particularly costly to produce (handicap hypothesis) or biochemically linked to reproduction (index hypothesis). There is tantalising evidence that alkanes with a methyl group on the third carbon (like 3-MeC₃₁) are also queen pheromones in other species of social insects. 3-methylalkanes have been correlated with fertility and/or caste in other highly-social Formicine ants (*Camponotus floridanus*²⁵ and *Formica fusca*²⁶) and in more basal ants (*Myrmecia gulosa*,²⁷ *Diacamma ceylonese*,²⁸ *Pachycondyla inversa*²⁹ and *Platythyrea punctata*³⁰). Even more surprisingly, these compounds are characteristic of reproductives in the distantly-related termites³¹ and have been indirectly linked to the regulation of worker reproduction in the wasp *Ropalidia marginata*.³²

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