



# The evolution of cuticular fertility signals in eusocial insects

Adrian A Smith<sup>1,2</sup> and Jürgen Liebig<sup>3</sup>

A reproductive division of labor is a definitive characteristic of eusocial insect societies and it requires a means through which colony members can assess the presence and productivity of reproductive individuals. Cuticular hydrocarbons are the primary means of doing so across eusocial hymenopterans. However, recent experimental work presents conflicting views on how these chemical signals function, are interpreted by workers, and evolve. These recent advances include demonstrations of hydrocarbons as evolutionarily conserved 'queen pheromones' and as species-divergent 'fertility signals' used by both queens and workers. In this review, we synthesize conflicting studies into an evolutionary framework suggesting a transition of reproductive communication from cue-like signature mixtures, to learned fertility signals, to innate queen pheromones that evolved across eusocial insects.

## Addresses

<sup>1</sup> Research & Collections, North Carolina Museum of Natural Sciences, 11 W. Jones St, Raleigh, NC 27601, USA

<sup>2</sup> Department of Biological Sciences, North Carolina State University, Raleigh, NC, USA

<sup>3</sup> School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

Corresponding author: Smith, Adrian A  
([Adrian.Smith@naturalsciences.org](mailto:Adrian.Smith@naturalsciences.org))

Current Opinion in Insect Science 2017, 22:79–84

This review comes from a themed issue on **Social insects**

Edited by **Amy Toth** and **Adam Dolezal**

<http://dx.doi.org/10.1016/j.cois.2017.05.017>

2214-5745/© 2017 Elsevier Inc. All rights reserved.

## Introduction

Societies of eusocial insects are pinnacles of social organization and are based on a reproductive division of labor between reproducing individuals, usually queens and helper workers. Despite this central organizing principle, these societies vary widely. They range from small colonies with simple organizations to highly complex societies with millions of colony members. Along with the increase of colony size, colony characteristics, such as physiological differences between reproductive castes, change [1] as do

the mechanisms used to maintain a reproductive division of labor.

This division can be organized through many mechanisms, such as dominance contests between physiologically equivalent individuals [2] or through anatomical and physiological specialization [3]. Regardless of how the division of labor is established, maintenance of it requires a means of assessing the presence and productivity of reproductive individuals. The main mechanism of assessing reproductive status in eusocial insects is through chemical communication [4–6]. Reproductive individuals are hypothesized to produce honest signals of their reproductive status rather than compounds that actively manipulate reproductive efforts of nestmates [4–6]. Correspondingly, recent reviews of the literature that have focused on the question of signal honesty found little evidence of dishonesty and queen manipulation of workers [6–9]. The responses to receiving these signals include self-restraint of ovary development and egg laying (a primer effect) and active behavioral suppression of nestmate reproduction through egg eating or physical aggression (a releaser effect) [10]. Both of those worker responses have been used as the means of experimentally identifying which chemical compounds or blends of compounds constitute reproductive signals.

Although correlational studies linking cuticular hydrocarbons (CHCs; a layer of non-volatile waxes coating the surface of an insect) to reproductive activity are numerous (comprehensively reviewed in Ref. [11]), experimental identification of these compounds as signals of reproductive activity has only recently been performed for eusocial hymenopterans [11–16,17<sup>\*\*</sup>,18<sup>\*\*</sup>,19<sup>\*\*</sup>,20]. Additionally, correlational data link CHCs to reproductive activity in termites [21,22]. Beyond eusocial insects, CHCs are omnipresent across insects serving as a means of desiccation resistance, and many solitary insect groups use hydrocarbons for species and mate recognition [23]. It is worth noting here that non-CHC sources of signals that regulate reproduction in eusocial insects have also been identified, such as the multicomponent queen-mandibular pheromone of honey bees [24] and a volatile queen and egg pheromone of *Reticulitermes* termites [25]. The Dufour's gland in ants is a known source of chemicals used by either a primary reproductive [26] or a queen [27] to induce punishment from workers towards subordinate reproductive nestmates. This gland is also the source of queen signaling hydrocarbons, similar to CHCs, in the wasp *Ropalidia marginata* [28]. Finally,

recently discovered dialkyl-tetrahydrofuran compounds that are mixed within queen CHC profiles and likely used for queen recognition in a trap-jaw ant [17\*\*].

This review focuses on CHCs as reproductive signals of eusocial insects. Just within the past two years several reviews dealing with this topic have been published [7,29–32]. Therefore, the aim of this brief review is not to retread this topic through a comprehensive approach. Instead, we narrow our focus on an outstanding problem involving seemingly conflicting experimental studies of how CHCs are interpreted as reproductive signals. Our goal is to present a new evolutionary framework that incorporates these conflicting recent studies and provide a new cohesive view of how cuticular chemical signaling of reproductive status evolves across insect societies.

### Queen pheromones vs. fertility signals: are they different?

In the literature, CHCs that signal the presence and productivity of reproductive individuals are most commonly referred to as ‘queen pheromones’ and less commonly ‘fertility signals’. While the terms are often used interchangeably, some researchers have begun to point to useful distinctions [33\*\*]. Common usages of the term ‘queen pheromone’ describe CHC compounds produced by queens that have a primer effect on workers, inhibiting ovary development and egg laying. Workers encounter these queen pheromones when in proximity to the queen or queen-produced brood [34,35\*,36,37]. Queen-laid eggs that are coated with queen pheromones provide means for queens to advertise their presence in the colony and a means for workers to discriminate queen-laid from worker-laid eggs, destroying the latter [35\*,36,37]. To date, all of the experimental evidence for queen CHCs having a primer effect on worker reproduction has been gathered through an assay used to identify the queen pheromone of *Lasius niger* ants [13]. Workers are separated from their queen and exposed to a hydrocarbon compound that is indicative of a queen-specific CHC profile. Daily treatments of the hydrocarbon are made through either introduction of a compound-treated piece of glass [13] or direct application of compound-solvent solution onto the nest substrate [20]. After weeks of treatments, workers are frozen and dissected for measurements of ovary development [11]. Worker ovaries from treatment nests are compared to control nests given sham or non-queen hydrocarbon treatments. Queen hydrocarbons have been found to reduce ovary activation relative to controls in several species of ants [11,13,14,19\*\*], the bumblebee *Bombus terrestris* [11,38,39], and two wasps [11,20]. Notably, using this assay, queen hydrocarbons were found to have no effect on inhibiting worker reproduction in the bumblebee *Bombus impatiens* [33\*\*] and the ant *Odontomachus brunneus* [18\*\*]. Furthermore, a recent experiment demonstrated that caged *B. impatiens* queens

fail to inhibit worker ovary development, suggesting that exposure to queen chemicals alone is insufficient for inhibition of worker reproduction [40].

The term ‘fertility signal’ is commonly used to refer to changes in CHCs that correlate with fertility, which nestmates use to assess the reproductive status of one another. Though CHCs identified as queen pheromones can fit this description [12,33\*\*], ‘fertility signals’ is also used to describe worker-produced CHCs that correlate with worker ovary development and egg laying [41]. These CHCs are a means of detecting and punishing reproductive workers in the presence of a queen (or a dominant egg-layer) [15]. In queenless conditions, these signals garner reproductive individuals queen-like treatment from nestmates [16]. Experimental identification of worker-produced CHC fertility signals is available for *Odontomachus* [16,17\*\*,18\*\*] and *Novomessor* [15] ants, and relies on measurements of these releaser-effects (aggression, and queen-respondent submissive behaviors) towards non-reproductive workers whose CHC profile is supplemented with fertility-correlated compounds. Additionally, many correlational studies link worker reproductive activity to CHC changes across social insect taxa [11]. A notable exception is found in some advanced eusocial species with high degrees of worker-queen dimorphism, where workers are reported to not exhibit any fertility-associated changes in CHC profiles [37,42]. When CHCs are used as fertility signals by both queens and workers, there has yet to be an experimental identification of worker-produced reproductive signaling compounds that are different than what queens use.

The similarity between queen and worker produced fertility signals may be evidence that CHC ‘queen pheromones’ are a derived condition of ‘fertility signals’ once used by all members of the colony. Queen castes and large colony sizes are derived conditions of eusocial groups. ‘Queen pheromones’ with primer effects are not likely to have been present or needed in early eusocial evolution. Group sizes were small and either dominance interactions between nestmates regulated a reproductive division of labor [1] or workers were able to recognize reproductive individuals without fertility signals. The ontogeny of colonies might reflect these ancestral conditions, for example, queens in incipient colonies of *Camponotus floridanus* do not yet produce fertility-specific CHCs, while in large colonies CHCs prominently distinguish highly fertile queens from workers and most likely represent queen pheromones [43,44].

We hypothesize that along with increased colony size and reproductive specialization, stronger and more refined reproductive signals are selected to convey the presence of a fertile reproductive to all the workers which leads to adaptations in receiver signal discrimination and sensory

Download English Version:

<https://daneshyari.com/en/article/5761106>

Download Persian Version:

<https://daneshyari.com/article/5761106>

[Daneshyari.com](https://daneshyari.com)