



Inter-caste communication in social insects

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Social insect colonies function as highly integrated units despite consisting of many individuals. This requires the different functional parts of the colony (e.g. different castes) to exchange information that aid in colony functioning and ontogeny. Here we discuss inter-caste communication in three contexts, firstly, the communication between males and females during courtship, secondly, the communication between queens and workers that regulate reproduction and thirdly, the communication between worker castes that allows colonies to balance the number of different worker types. Some signals show surprising complexity in both their chemistry and function, whereas others are simple compounds that were probably already used as pheromones in the solitary ancestors of several social insect lineages.

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Current Opinion in Neurobiology 2016, **38**:6–11

This review comes from a themed issue on **Neurobiology of sex**

Edited by **Barry J Dickson** and **Catherine Dulac**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 21st January 2016

<http://dx.doi.org/10.1016/j.conb.2016.01.002>

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Introduction

Insect colonies often consist of thousands — and sometimes millions — of individuals and the success of individuals depends crucially on the success of the colony [1,2]. Colonies show two kinds of division of labor. First, there is a reproductive division of labor between queens (and kings in termites) and the largely sterile workers. Second, there is division of labor among the workers for tasks like brood rearing, colony defense or foraging [1,2]. Communication between and within the different castes (queens, males and different worker groups) is fundamental for the efficient functioning of a colony. In order for colonies to respond to the often changing needs, workers — like the cells of multicellular organisms — need to respond to signals in ways that are beneficial to the whole complex system.

Most communication is based on chemical signals (or pheromones) that are produced by exocrine glands [1–4]. Hundreds of chemicals produced in more than 60 different glands have been identified in social insects [3,5], which has led researchers to refer to social insects as chemical factories [1]. Traditionally, pheromones have been divided into two classes, primer and releaser pheromones [1]. A releaser pheromone initiates an immediate behavioral response, whereas a primer pheromone alters more long-term endocrine and reproductive systems in the recipient [6]. However, it has become clear that there are pheromones that have both releaser and primer effects [6–8]. The pheromone signals are perceived via olfactory sensillae on the antennae [3,9,10*,11*] before being further processed by the olfactory system [12].

In this review we focus on recent advances in our understanding of inter-caste communication in three important contexts: firstly, communication between male and female reproductives that results in mating and, subsequently, colony foundation, secondly, communication between queens and workers to regulate reproduction and thirdly, communication between different functional groups of workers (sometimes called sub-castes) that allows colonies to balance the number of workers performing different tasks (for communication within castes, for example, among foragers during resource collection or during house hunting see [13–16]). Recent research has highlighted the importance of chemical and behavioral complexity, context, and dose for communication [6]. Furthermore, the recent identification of several queen signals that inhibit reproduction in workers [7,17**,18] or other queens [19] has improved our understanding of the evolution of reproductive division of labor. New tools like calcium imaging or genomics have started to reveal how pheromone signals are processed in the nervous system [12,20] and how external cues and signals induce important behavioral modifications that are associated with large scale changes in the pattern of gene expression in the brain (e.g. [20–22]).

Communication between males and females

Before starting a new colony reproductive individuals must find a mating partner. Chemical communication plays a fundamental role in this process and males in particular show numerous adaptations that help them find females [3]. These include large compound eyes, strong wing muscles or antennae with large numbers of odor receptors [23,24]. Most mating patterns fall into two broad categories, the ‘female calling syndrome’ and the ‘male aggregation syndrome’ [1,3]. In species with the ‘female calling syndrome’, females are often wingless and do not travel far from their natal nest (sometimes they call from

within the nest). They release sex pheromones to ‘call’ the winged males. These species typically form small colonies and mating flights do not seem to be synchronized across colonies. In some cases it is the workers that ‘call’ males. In *Megaponera analis*, for example, males follow recruitment trails laid by workers to guide them to the nest [1]. In the stingless bee *Scaptotrigona postica*, 2-alcohols attract males from long range, but additional substances are then required to elicit copulations by males [25]. Once males have settled near a nest containing a virgin queen, the males themselves become attractive to other males, leading to large aggregations (Figure 1a) [26,27]. Thus, male aggregations in many stingless bee species are probably the outcome of both female and male calling [26–28].

Species with larger colonies frequently exhibit a ‘male aggregation syndrome’, whereby males from many colonies gather at specific sites where they are later joined by

females [3]. In these species mating flights are usually tightly synchronized between many colonies thereby decreasing the probability of inbreeding and hybridization between closely related species. In species such as some *Camponotus*, *Atta* and *Acromyrmex*, the departure of both sexes from the nest is coordinated by the release of mandibular pheromones by males as they leave the nest. This, in turn, triggers the mass exodus of females [3]. Honey bee (*Apis mellifera*) drones gather at congregation areas (ranging from 30 to 200 m in diameter) where they wait for virgin queens [23,29]. A modification to this pattern of male aggregations is found in bumble bees where males patrol flight paths which they mark with labial gland secretions [30]. In *Bombus terrestris*, and probably other *Bombus* species, females are preferentially attracted to flight paths marked by many males, hence selecting for males to aggregate to attract females [3]. Another alteration to the ‘male aggregation syndrome’ is found in many polistine wasps, where males mark objects in their territories with scent by dragging their legs or abdomens over the substrate or release pheromones into the air [31,32].

Figure 1



(a) A male aggregation in the Neotropical stingless bee *Tetragonisca angustula*. Aggregations of several hundred males are usually found close to a nest that contains a virgin queen or will soon contain a virgin queen (Photo by C. Grüter). (b) A fire ant (*Solenopsis invicta*) queen and her retinue workers. The workers feed and groom the queen and remove her eggs (Photo by W.R. Tschinkel).

How females locate male aggregations is not well understood but males’ mandibular glands have been implicated as the source of the sex attractant in numerous ant genera and conclusively demonstrated in several *Pogonomyrmex* species [1,3]. The main compound found in mandibular glands in *Pogonomyrmex* (4-methyl-3-heptanone) seems likely to play an important role in female attraction [3], although controlled experiments are needed to confirm this. Once females have found the aggregation female-derived pheromones are thought to attract males at close range. In *Formica lugubris*, for example, the source of the attractant is the females Dufour’s gland, which contains undecane (90%), (Z)-4-tridecene (4%), and tridecane (4%). Synthetic undecane causes a strong male response similar to the response observed in nature [33]. One of the first identified sex pheromones is the honey bee ‘queen substance’, which originates from the queens’ mandibular glands [34]. Mandibular gland extracts of honey bee queens attract drones from a distance of ~50 m [3,29]. The most active compound (9-keto-(E)-2-decenoic acid or 9-ODA) is almost as active as the whole blend [34]. Interestingly, Asian honeybee species also use 9-ODA as the main male attractant [35]. However, differences in the timing and location of mating flights and visual cues of sexual partners seem to limit heterospecific sexual encounters [3]. After mating, queens of some species quickly become unattractive to males. This can be caused by changes in the queens’ cuticular hydrocarbon (CHC) profile (e.g. *Leptothorax gredleri* [36]) or by tactile signals produced by the queen (e.g. *Pogonomyrmex* spp. [1]).

Communication between queen and workers

An important prerequisite for the functioning of social insect colonies is the ability of queens to signal their presence and good health. To this end queens produce a

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