

# Ecology and Evolution of Communication in Social Insects

Sara Diana Leonhardt,<sup>1,4</sup> Florian Menzel,<sup>2,4</sup> Volker Nehring,<sup>3,4</sup> and Thomas Schmitt<sup>1,\*</sup>

<sup>1</sup>Department of Animal Ecology and Tropical Biology, University of Würzburg, 97074 Würzburg, Germany

<sup>2</sup>Evolutionary Biology, Institute of Zoology, University of Mainz, 55128 Mainz, Germany

<sup>3</sup>Department of Evolutionary Biology and Animal Ecology, University of Freiburg, 79104 Freiburg, Germany

<sup>4</sup>Co-first authors

\*Correspondence: [thomas.schmitt@uni-wuerzburg.de](mailto:thomas.schmitt@uni-wuerzburg.de)

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**Insect life strategies comprise all levels of sociality from solitary to eusocial, in which individuals form persistent groups and divide labor. With increasing social complexity, the need to communicate a greater diversity of messages arose to coordinate division of labor, group cohesion, and concerted actions. Here we summarize the knowledge on prominent messages in social insects that inform about reproduction, group membership, resource locations, and threats and discuss potential evolutionary trajectories of each message in the context of social complexity.**

## Introduction

Communication in social insects has fascinated scientists for centuries. One of the most famous examples is the dance language of honeybees. Karl von Frisch showed that honeybees dance in order to inform their nestmates about the location of resources (von Frisch, 1967), a breakthrough for which he was granted the Nobel Prize in 1973. Since then, our understanding of the topics and mechanisms of communication in social insects has significantly advanced for a wide variety of species.

Insects show all levels of social organization, from solitary species where conspecific individuals rarely meet to eusocial species with large, persistent colonies, where groups of individuals (“castes”) perform different tasks (division of labor). The evolution of sociality in insects can be compared by analogy to other major evolutionary transitions, such as the evolution of multicellularity. For example, the division of labor in eusocial insects resembles the diversification of cells that take over specific tasks in a multicellular organism. Just as somatic cells are disposable and reproduction is restricted to germline cells, there is division of labor between social insect workers and royals (Boomsma, 2013). And just like separate organs communicate using hormones, individuals in insect societies use pheromones as messengers. The diversity of information, i.e., the number of different messages that become encoded by signals, increases with the complexity of social organization.

In this Review, we give an overview of the current knowledge on intraspecific communication in social insects, defined as the transfer between individuals of information that is either mutually beneficial or beneficial for one and neutral for the other participant. We provide insights into the evolution of the messages used by social insects and discuss how their diversity increased with the evolution of social complexity.

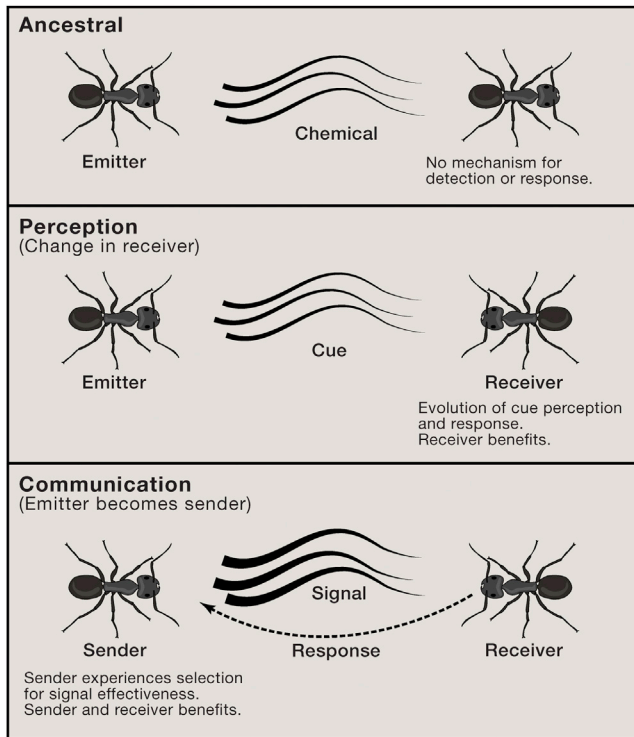
## Evolution of Communication with Sociality

The oldest mode of communication is the transfer of chemicals (Wyatt, 2014). Chemical communication evolves when individ-

uals start to detect substances emitted by other individuals. At that stage the chemicals effectively become “cues.” Cues are informative traits of individuals that are unintentionally presented by an emitter and used by a receiver to infer information about the emitter (Figure 1). When receivers respond and emitters benefit from the receivers’ responses, emitters evolve more sophisticated and reliable “signals,” i.e., co-evolved traits intended to transfer information; this is defined as “true communication” (Figure 1) (Dusenbery, 1992). However, information provided by a sender can also be aimed at manipulating the receiver to its disadvantage (e.g., predators attracting prey by mimicking prey signals) or be exploited by a second receiver to the sender’s disadvantage (e.g., by parasites to locate hosts) (Steiger et al., 2011), rendering a precise definition of communication elusive.

Subsequently, in the animal kingdom signaling modes beyond chemicals evolved, including acoustic/vibrational, visual, and tactile communication. In insects, chemical cues and signals (pheromones) still dominate, although all other modes of communication occur (Bradbury and Vehrencamp, 2011; Wyatt, 2014) (Figure 2).

Both solitary and social insects communicate. In strictly solitary insects, communication is largely restricted to sexual context and involves signals that attract and inform mating partners, frequently with a multitude of signals transferred between mating partners during courtship. The most prominent and widespread examples for such signals are sex pheromones (single substances or blends of chemicals) (Wyatt, 2014), which are largely species and sex specific to ensure mating with an appropriate partner. Sexual signals can also be visual, acoustic/vibrational, or tactile or involve multiple communication modes, e.g., chemical and tactile/visual signals such as those used for mating in *Drosophila melanogaster* (Bontonou and Wicker-Thomas, 2014). Mating signals can also bear information on kinship so individuals can recognize each other’s relatedness and avoid inbreeding (Lihoreau et al., 2007).



**Figure 1. Proposed Stages in the Evolution of Chemical Communication in Insects**

Ancestrally, chemicals are unintentionally emitted by an individual (emitter) and not detected by any other individual. If another individual (receiver) evolves the capability to perceive the unintentionally emitted chemical and benefits from the transferred information, the chemical becomes a cue. If there is additional advantage to the emitter from receiving reciprocal information, the emitter becomes a sender and the cue a signal, and this can be considered “true communication.” Adapted from Wyatt (2014), with image by Ivan Hinojosa ([www.flickr.com/photos/ivan\\_hinojosa](http://www.flickr.com/photos/ivan_hinojosa)).

As insects evolved higher levels of sociality, the information they needed to exchange between group members diversified to include division of labor, collaborative resource utilization, and collective defensive actions (Figures 3 and 4). This trend is reflected in the diversity of chemical signals required to maintain eusocial insect colonies (Box 1). However, it is important to note that increased message diversity does not necessarily correlate with increased complexity of the signals themselves (Kather and Martin 2015). Indeed, signals used in solitary insects are in some cases more complex in terms of composition than some signals used in social insects, and pheromone signals in social insects most likely evolved from systems regulating more basal behaviors in solitary insects (Blum, 1969) (Figure 5). For example, although kin recognition is important for solitary insects to avoid inbreeding, in insects with brood-care, kin recognition is expected to play an even more important role to prevent parents from feeding or protecting someone else’s offspring. However, kin recognition has rarely been shown (Linsenmair, 1987). Instead, most species seem to employ rules of thumb whenever simpler cues suffice. Illustrating this point, parents of the subsocial burying beetle *Nicrophorus vespilloides* (Figure 4A) cannot discriminate between their own and artificially introduced larvae

but accept all brood that is of the right age (calculated from time of egg laying) (Steiger, 2015).

Signals such as aggregation pheromones that help individuals to find each other, dispersion pheromones that disassemble groups (Heifetz et al., 1998), alarm signals, and recruitment signals that guide group members to resources are important tools for supporting insect societies. Group gathering can be accomplished by species-specific long-range aggregation pheromones that attract both sexes of a species (Figure 4B). Here, the most prominent and best studied examples are insect pest species, e.g., gregarious bark beetles, which use species-specific aggregation pheromones to overcome a tree’s defense in a concerted action (Byers, 1989).

In the most derived insect societies, reproduction is monopolized by one (or few) individual(s) (“queens”/“kings”), whereas the others (“workers”) perform foraging, nest maintenance, and nursing duties (eusociality; Figure 4D).

Below we highlight four types of messages typically used in eusocial insect colonies: queen signals (which organize reproductive division of labor), nestmate recognition (which ensures group cohesion), recruitment, and alarm signals (both of which organize concerted group actions). We discuss evolutionary trajectories of each message in the context of social complexity and finally suggest future directions to better understand the evolution of communication in insect societies.

### Queen Signaling

Signals produced by queens in eusocial colonies indicate the queen’s presence and/or fertility to workers who then abandon their own reproduction and help with rearing siblings (Keller and Nonacs, 1993) (Figure 4D). Workers can further use this information to control each other’s reproduction by for instance destroying eggs laid by other workers (egg policing: Ratnieks, 1988; Ratnieks and Reeve, 1992). When a colony loses its queen or the queen loses fertility, the queen signal diminishes and non-sterile workers can start laying eggs themselves (Keller and Nonacs, 1993). Consequently, communicating the presence and fertility of a queen reinforces reproductive division of labor and benefits the social organization within colonies.

### Signals Used

In species with small colonies (<100 individuals), queen signals can comprise aggressive queen-worker interactions and even visual signals in addition to chemical signals (Tannure-Nascimento et al., 2008). In contrast, large colonies (several 100 individuals) typically rely entirely on chemical signals, the so-called queen pheromones (Hölldobler and Wilson, 1990; Keller and Nonacs, 1993). In very large colonies (>1,000 individuals), information about the queen’s presence and fertility is further communicated indirectly, e.g., through messenger workers who spread the queen pheromone in the colony (e.g., in the honeybee: Naumann et al., 1991) or through a specific chemical signature on queen-laid eggs (Endler et al., 2004).

Queen pheromones are likely present in most eusocial insect species and are thought to be located on the queen’s cuticle (Monnin, 2006; Oi et al., 2015). Different species appear to use different (albeit partly structurally related) compounds as queen pheromones (Kocher and Grozinger, 2011; Oi et al., 2015). However, only a few studies experimentally demonstrated that

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