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REVIEW ARTICLE

Intracolony chemical communication in social insects

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Abstract Chemical messengers are the primary mode of intracolony communication in the majority of social insect species. Chemically transmitted information plays a major role in nestmate recognition and kin recognition. Physical and behavioral castes often differ in chemical signature, and queen effects can be significant regulators of behavior and reproduction. Chemical messengers themselves differ in molecular structure, and the effects on behavior and other variables can differ as a consequence of not only molecular structure of the chemical messenger itself but also of its temporal expression, quantity, chemical blends with other compounds, and effects of the environment. The most studied, and probably the most widespread, intracolony chemical messengers are cuticular hydrocarbons (CHCs). CHCs are diverse and have been well studied in social insects with regard to both chemical structure and their role as pheromones. CHCs and other chemical messengers can be distributed among colony members via physical contact, grooming, trophallaxis, and contact with the nesting substrate. Widespread intracolony distribution of chemical messengers gives each colony a specific odor whereby colony members are integrated into the social life of the colony and non-members of the colony are excluded. Colony odor can vary as a function of genetic diversity within the colony, and the odor of a colony can change as a function of colony age and environmental effects. Chemical messengers can disseminate information on the presence of reproductives and fertility of the queen(s) and workers, and queen pheromone can play a significant role in suppressing reproduction by other colony members. New analytical tools and new avenues of investigation can continue to expand knowledge of how individual insects function as members of a society and how the society functions as a collective.

Keywords Colony closure · Colony cohesion · Colony odor · Cuticular hydrocarbons · Kin recognition · Nestmate recognition · Pheromones · Social interactions

> *[The antenna of the ant is] covered with olfactory, tactile (or aural) organs, able to taste, touch, and hear all sides of an object at once, without division or separation, without lapse of time between one mode of apprehension and another.*
>
> from *The Feel of the Smell Itself* by Mary Mackey Colwell
> (Mary Mackey Colwell is a pseudonym for Mary Mackey, used with permission)

Introduction

Communication among members of a social group is necessary to delineate group membership, coordinate activities, and identify castes or individuals and their roles in the society. Indeed, without communication there could be no

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society. Social communication can be chemical, visual, acoustical, tactile, or substrate-borne. The most common mode of communication in social insects is chemical, and one of the challenges in the study of chemical communication is to understand the cues and signal patterns involved in colony cohesion that are essential for recognition of species, populations, colonies, castes, and individuals. Elucidation of the mechanisms underlying these different types of recognition is crucial to our understanding of communication between social insects and the evolutionary advantages they may confer (Hölldobler and Wilson, 1990).

Chemical communication is the most ancient and widespread sensory information mode in animals (Candolin, 2003). It is efficient under almost all conditions and can be a rapid and efficient mode of disseminating information concerning traits such as sex recognition, sexual receptivity, health status, motivation to fight, dominance, and task-specificity. Most social insects employ chemicals as their major mode of communication to coordinate important life processes. Social insects can be thought of as "chemical factories" due to their high number of exocrine glands (Billen and Morgan, 1998). At least, 75 anatomically distinct exocrine glands have been found across all ant species (Billen, 2011). The exocrine glands of social insects produce diverse chemicals, collectively called semiochemicals, which have intraspecific (pheromonal) and/or interspecific (allelochemical) actions (Glossary box). Colony activities are often coordinated via pheromones, and in some cases individuals can change the meaning of transmitted information by varying the concentration of a pheromone or by mixing pheromones from multiple glands (Billen, 2011).

The capacity to recognize nestmates is well developed in most social insect species (Crozier and Pamilo, 1996), and the majority of social insects use chemical communication in doing so. The ability to distinguish familiar nestmates from unfamiliar intruders can trigger agonistic defensive behaviors directed toward intruders, which can be either allospecific or non-nestmate conspecific, and thereby maintain colony integrity and colony closure (Glossary box). Nestmate recognition is a vital adaptation with strong selective pressure for accuracy. For example, nestmate recognition and aggressive behavior are needed to prevent robbers from stealing honeybees' colony resources (Seeley, 1985). Colony closure can be based on different recognition systems. One hypothesis is that workers discriminate nestmates from unfamiliar intruders by comparing intruders' odor with a template of the colony odor and reject individuals carrying unfamiliar cues while admitting individuals with familiar cues (Guerrieri et al., 2009), a "desirable-present" system (Sherman et al., 1997). In a second hypothesis, inspection of an individual's odor could be to search for undesirable cues that are independent of the presence of desirable cues to determine acceptance or rejection, an "undesirable-absent" system (Couvillon and Ratnieks, 2008).

Chemical nestmate discrimination systems in social insects are based primarily on cuticular hydrocarbon compounds (CHCs), and these have been described in many species (Martin and Drijfhout, 2009a; Ozaki and Wada-Katsumata, 2010 and reference therein). In addition to CHCs, peptides and proteins are present on the cuticle of social insects such as honeybees (Zupko et al., 1993), and these compounds could play a role as pheromones. Although cuticular peptides are potentially involved in nestmate recognition, chemical analyses and behavioral observations show that polar cuticular compounds such as peptides are not colony-specific and not involved in colony recognition cues (Bruschini et al., 2011). Similarly, even though cuticular peptide patterns may vary with reproductive status and age in termites (Hanus et al., 2010), they do not play a role in intracolony recognition cues (Dapporto et al., 2008).

Several reviews on the roles of semiochemicals in social insects will be mentioned in this review, but none of these have compared chemical communication in all intracolony aspects across the four major taxa of social insects: termites, social wasps, ants, and social bees. Eusociality evolved independently in these taxa, noneless they evolved similar modalities and patterns of chemical communication (Brady et al., 2006; Hines et al., 2007; Nowak et al., 2010). In addition to comparisons across taxa, the review highlights proximate factors that influence intracolony chemical communication. A comparative approach and attention to proximate factors can enhance an understanding of the evolution, success, and maintenance of chemical communication in insect societies. Topics included in this review are chemical messengers themselves, behaviors that transmit chemical information, recognition of nestmates and kin, environmental effects, castes and task specialization, and queen effects on colony cohesion.

Chemical communication is also a significant component of alarm reactions, recruitment to food sources, nest finding, and territoriality (Hölldobler and Wilson, 1990), but because this review focuses on within-colony chemical communication between individuals or via the nesting substrate, these topics are not covered here. The review emphasizes behavioral contexts for chemical modalities in the intracolony life of these social insects, with a target readership of social insect biologists broadly rather than specialized chemical ecologists. Vibroacoustic modalities of intracolony communication, which also play significant roles in social insects, are treated in a companion review (Hunt and Richard, in press).

Origin and dynamics of colony label recognition cues

Genetic diversity plays a role in nestmate, matriline and patriline recognition

Genetic diversity varies between species and among populations of a single species. In social insects genetic diversity can also vary among nestmates (Ross, 2001), depending on the number of queens and their mating history: monogyny, polygyny, monandry, and/or polyandry. Components of chemical recognition cues can be inherited, therefore polygyne colonies with different matrilines possess greater cue diversity than monogyne colonies (Vander Meer and Morel, 1998). This is reflected in workers from polygyne colonies being less aggressive toward intraspecific non-nestmates than are workers in monogyne colonies (Bennett, 1989; Sundström, 1997), which could be due to subtle differences of chemical profiles between monogyne and polygyne workers (Lin et al., 2010). A correlation between aggression and genetic distance between workers from different colonies and different populations exists in the polygynous and polydomous ants *Formica polyctena* and *F. pratensis* (Beye et al., 1997; Beye et al., 1998). However, the degree of colony social closure and genetic diversity are not correlated in the socially polymorphic (both monogyne and polygyne colonies) species *F. selysi* (Rosset et al., 2007).

Chemical communication could play a significant role in the evolution of ant unicoloniality (Helanterä et al., 2009, Glossary box). In the Argentine ant, *Linepithema humile*, comparative studies between native and introduced populations suggest that loss of genetic diversity and correspondingly lower levels of aggression could be primarily responsible for the evolution of unicoloniality (Tsutsui et al., 2000). Unicoloniality could also be due to selective mixing of non-nestmates that share high levels of phenotypic similarity (Giraud et al., 2002). A correlation of between-colony similarity in CHC profiles of both workers and queens and between-colony genetic similarity (Vasquez et al., 2009) could be a proximate factor that facilitates colony fusion. Nestmate recognition cues and the production of CHCs are influenced by genetic background in the Argentine ant and three other unicolonial species in the genus *Temnothorax* (Tsutsui et al., 2000; Suarez et al., 2002; Tsutsui et al., 2003; Foitzik et al., 2007). Unicoloniality does not always depend on genetic similarity, however, as it also exists in highly polygyne species such as *Formica paralugubris* in which individuals discriminate among nestmates (Holzer et al., 2006).

Many studies published before 2000 examined matriline and patriline discrimination in ant and wasp colonies without confirming such discrimination. However, different matrilines' cuticular compound profiles provide sufficient information for matriline discrimination in the wood ant *Formica truncorum* and the wasps *Polistes dominula* [*dominulus*] and *Vespa crabro* (Boomsma et al., 2003; Dani et al., 2004b). In monogyne colonies composed of different patrilines, full sisters and half sisters differ in their cuticular hydrocarbon profiles in *Acromyrmex octospinosus* (Nehring et al., 2011), *Formica truncorum* (Boomsma et al., 2003), *Formica exsecta* (van Zweden et al., 2011), the hornet *Vespa crabro* (Dani et al., 2004b), and several species of *Apis* honeybees (Getz and Smith, 1986; Arnold et al., 1996). Although the information conveyed by cuticular compounds may be accurate enough to permit potential within-patriline cooperation in *A. octospinosus*, the heritable component of recognition cues appears to be too weak and error-prone in *F. truncorum, F. exsecta*, and *V. crabro*. In honeybee colonies, which are monogynous and polyandrous, CHCs differ between patrilines (Arnold et al., 1996). It cannot be ruled out that patriline discrimination in honeybees exist due to different conclusions in data interpretation, and a study found no evidence for subfamily discrimination among honeybee dancers and their followers (Kirchner and Arnold, 2001).

The presence or absence of an efficient queen affects worker recognition

The role played by the queen in colony closure and colony recognition has been well documented in several species and has revealed a high variability among species.

The presence of the queen's pheromones that serve as recognition cues can influence nestmate recognition and intraspecific interactions in several ant species (Carlin and Hölldobler, 1987; Provost, 1987; Keller and Passera, 1989; Lahav et al., 1998; Vander Meer and Alonso, 2002). In orphaned *Solenopsis invicta* colonies, worker aggression toward non-nestmate conspecifics drops (but still exists with interspecific interactions) and re-establishes following acceptance of a newly mated queen (Vander Meer and Alonso, 2002). The new queen exposes workers to her queen primer pheromone, the level of which correlates with workers' sensitivity to colony-level differences in cuticular hydrocarbons. Increased sensitivity is linked to higher levels of octopamine in workers' brains of queenright colonies compared with orphan colonies (Vander Meer et al., 2008). However, the presence of the queen does not influence nestmate recognition cues in several other ant species (Boulay et al., 2004; Caldera and Holway, 2004; Richard et al., 2004; van Zweden et al., 2009).

Honeybee queens produce pheromones that act as releaser pheromones and regulate many aspect of colony organization, worker behavior, and physiology (Slessor et al., 2005; Le Conte and Hefetz, 2008); therefore, removal of the queen has dramatic consequences for colony functioning. Queenless workers exposed to queen mandibular pheromone have significantly different CHC profiles than those of queenright workers in the colony from which the queenless sample was taken. Bees of the queenright colony respond with agonistic behavior toward re-introduced bees from queenless fragments of the original colony, which are no longer recognized as nestmates even if treated with queen mandibular pheromone. However, queenright workers can discriminate re-introduced queenless nestmate workers treated with queen mandibular pheromone from non-nestmates (Fan et al., 2010).

Environmental factors affect nestmate recognition

Environmental factors including temporal and seasonal variation, nesting substrate, diet, social environment, and the presence of symbionts and pathogens can affect nestmate recognition. Colony odor can change seasonally and over the lifetime of a colony (Vander Meer et al., 1989; Bowden et al., 1998; Nielsen et al., 1999). For example, workers of the same *Formica truncorum* colony collected a few months apart had quantitative differences in individual CHC profiles (Nielsen et al., 1999).

Laboratory colonies live in different environments compared with conspecifics in their natural habitat, and they differ in both quantitative and qualitative CHC profiles. For example, in the harvester ant *Pogonomyrmex barbatus* the quantity of alkanes is higher in laboratory colonies (Tissot et al., 2001). Nesting substrate can influence chemical profiles used for nestmate recognition in the ants *Leptothorax nylanderi* (Heinze et al., 1996), *Acromyrmex octospinosus*, and *A. echinatior* (Richard et al., 2007a). Aggression tests show that workers of colonies maintained in the laboratory are less aggressive toward conspecific non-nestmates than field colonies (Obin, 1986; Obin and Vander Meer, 1988; Crosland, 1989). Nest substrate is also involved in wasp colony odor (Pfennig et al., 1983; Singer and Espelie, 1992; Gamboa et al., 1996; Singer and Espelie, 1996).

Recognition cues also can vary due to diet changes (Silverman and Liang, 2001; Richard et al., 2004; Sorvari et al., 2008). CHCs from prey newly present in a worker's chemical profile can alter nestmate recognition and elicit aggression from colony mates (Liang and Silverman, 2000; Liang et al., 2001). In the leaf-cutting ant *Acromyrmex subterraneus*, workers from divided colonies fed with leaves from different species than the mother colony are attacked by workers kept in their mother colony, whereas workers from divided colonies fed with the same diet as the mother colony are accepted by workers in their mother colony (Richard et al., 2004). Individual workers' CHC and postpharyngeal gland profiles were similar among experimental groups receiving the same diet, and even more similar between individuals from the same sub-group, thereby suggesting odor homogenization may occur via individual interactions including grooming and also via contact with the symbiotic fungus (Richard et al., 2004). In addition, workers of different colonies of *Acromyrmex octospinosus* fed with the same diet were less aggressive toward each other in comparison with workers from different colonies fed with different diets (Jutsum et al., 1979). These studies demonstrate a strong impact of leaf diversity on colony odor and the ants' capacity to update it via grooming (Richard and Errard, 2009). In *Formica aquilonia*, environmental changes due to anthropogenic action increase levels of colony aggression in correlation with increased differences in between-colony cuticular chemical profiles attributable to diet composition (Sorvari et al., 2008). Rearing colonies under uniform conditions and receiving the same food source diminishes aggressive behavior in *Solenopsis invicta* and the wasp *Polistes fuscatus* (Gamboa et al., 1986; Obin and Vander Meer, 1988) and favors colony fusion (Buczkowski et al., 2005).

The intestinal bacteria community composition in termites is diverse and colony-specific (Matsuura, 2001 and reference therein). Experiments with the termite *Reticulitermes speratus* revealed that changing the composition of the bacterial community changed the recognition behavior toward nestmates, resulting in aggressive behavior. Thus, gut symbionts play an important role in nestmate recognition (Matsuura, 2001), but the proximate mechanisms involved in recognition pattern changes remain unknown.

Chemical aspects of nestmate recognition

The insect cuticle is covered by a layer of waxy substances that provide waterproofing. This waxy layer consists predominantly of lipids and contains aldehydes, alcohols, esters, fatty acids, and hydrocarbons (Fig. 1). Among CHCs (Glossary box) *n*-alkanes are often the dominant group and have a key role in reducing water loss due to their high melting point and structure (Gibbs, 1998), whereas alkenes are believed to be inefficient waterproofing compounds (Gibbs, 1995). High levels of *n*-alkanes are associated with species living in arid environments (Hadley and Schultz, 1987), and in a number of ant species *n*-alkanes are produced in higher quantities by foragers than nest workers (Wagner et al., 1998; Martin and Drijfhout, 2009b). Honeybee foragers have more *n*-alkanes than newly emerged and nurse bees (Kather et al., 2011), indicating protection from water loss for the foragers. In addition to a role in waterproofing, CHCs convey information about species identification, sex recognition, nestmate recognition, task-specificity (morphological and behavioral caste, fertility, age), and health

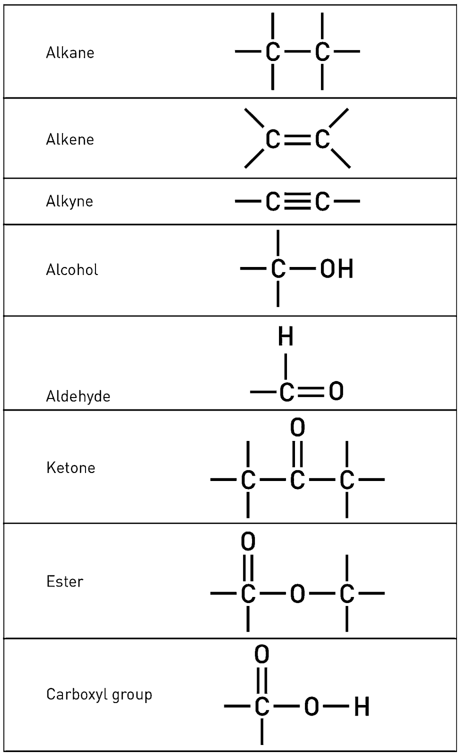

Fig. 1 Chemical structure of the organic compounds

(De Biseau et al., 2004; Howard and Blomquist, 2005; Monnin, 2006; Richard et al., 2007a; Richard et al., 2007b; Richard et al., 2008; Nunes et al., 2009; Weil et al., 2009; Blomquist and Bagnères, 2010; Backx et al., 2012; Borges et al., 2012; Richard et al., 2012).

Cuticular hydrocarbons play the major role in kin recognition

Nestmate discrimination is generally based on complex mixtures of CHCs (Boomsma and Franks, 2006). Perception of CHCs usually is possible at a short distance, but can necessitate direct contact to enable perception of components with no or low volatility (Brockmann et al., 2003; Brandstaetter et al., 2008), although analysis at high temperature reveals volatile properties of alkanes of up to 29 carbons in honeybee foragers (Schmitt et al., 2007). The diversity and proportions of CHCs play a fundamental role in colony and nestmate recognition cues in wasps (Dani et al., 1996; Lorenzi et al., 1997; Ruther et al., 1998; Panek and Gamboa, 2000; Dani et al., 2001; Sledge et al., 2001; Cervo et al., 2002; Tannure-Nascimento et al., 2007), in honeybees (Breed, 1998b), in ants (Lahav et al., 1999; Boulay et al., 2000; Akino et al., 2004; Richard et al., 2004; Greene and Gordon, 2007; Richard et al., 2007a; Martin and Drijfhout, 2009a), and in termites (Kaib et al., 2004; Dronnet et al., 2006).

CHC blends are diverse, with each species generally possessing a unique CHC profile (Richard et al., 2007b; Martin and Drijfhout, 2009a) and each colony of that species having a unique chemical signature characterized by differences in the mixture of the hydrocarbon groups. Foreign CHC mixtures elicit agonistic behavior (Greene and Gordon, 2007; Torres et al., 2007; Yusuf et al., 2010), and acceptance of introduced unrelated foragers workers by guards can be experimentally facilitated by washing the CHCs from the foragers (Breed et al., 2004). In most cases, nestmate recognition is linked to a mixture of CHCs, but in *Formica japonica* and *F. exsecta* Z9-alkenes are key nestmate recognition components (Akino et al., 2004; Martin et al., 2008). The role of these compounds in colony signature was confirmed by topical application on live ants of both naturally occurring and synthetic compounds that resulted in increased aggression directed toward coated nestmates (Martin et al., 2008). Several social insect species have homologous hydrocarbons with different carbon chain lengths but the methyl group is in the same position. In *Linepithema humile,* topical application of worker CHC extract enriched of one out of eight different synthetic compounds revealed differences in aggressive behavior according to the chain length with the same branch position and also to the branch position when the chain length is identical (van Wilgenburg et al., 2010).

Martin and Drijfhout (2009a) found no association between CHC profile and phylogeny. In contrast, a phylogenetic analysis by van Wilgenburg et al. (2011) indicates gradual evolution of CHC profiles, reveals structural types of CHCs occur only in some ant species, and suggests abrupt evolutionary transitions in the biosynthetic pathway of different lineages.

In wasps, chemically washed non-nestmates were attacked less than unwashed non-nestmates (Lorenzi et al., 1997; Cervo et al., 2002). CHCs washed from single individuals of the wasps *Polistes dominula* [*dominulus*], *P. biglumis bimaculatus*, *Liostenogaster flavolineata*, and *Vespa crabro* that then were reapplied on either dead or on washed living individuals, and also the application of synthesized hydrocarbons on the cuticles of workers, revealed that some CHC structural groups play a greater role in recognition than others (Dani et al., 1996; Lorenzi et al., 1997; Ruther et al., 1998; Dani et al., 2001; Sledge et al., 2001; Cervo et al., 2002). Topical application on live wasps of methyl-branched alkanes or alkenes elicits agonistic behavior when treated wasps enter the colony, but similar behavior does not occur in response to *n*-alkanes (Dani et al., 2001). In addition to playing a role in species, colony, and nestmate recognition, CHCs have been shown to mediate discrimination among individuals (Breed, 1998a; Howard and Blomquist, 2005).

Behavioral mechanisms for chemical circulation

Cuticular hydrocarbons are transferred within and among individuals

Insect hydrocarbons are synthesized by specific cells called oenocytes (Martin and Ramalho-Ortigao, 2012) in the fat body of adult insects (Ferveur et al., 1997; Fan et al., 2003). In several insects including ants, newly synthesized hydrocarbons are internally transferred by lipophorin to storage tissues and organs including the cuticle and the postpharyngeal gland (Van der Horst, 1990; Soroker and Hefetz, 2000; Schal et al., 2001). Newly synthesized hydrocarbons move bidirectionally between the cuticle and the postpharyngeal gland during both selfgrooming and allogrooming (Dahbi et al., 1999; Soroker and Hefetz, 2000; Lucas et al., 2004). During selfgrooming, hydrocarbons accumulate on the basitarsal brushes and then are transferred to the postpharyngeal gland as the forelegs are groomed. Subsequently, the hydrocarbons are distributed among all colony members via allogrooming, as described for *Pachycondyla apicalis* (Hefetz et al., 2001; Soroker et al., 2003). Full understanding of the transport and the deposition of hydrocarbons remains a challenge for future research (Bagnères and Blomquist, 2010).

Trophallaxis and allogrooming distribute chemicals used for colony odor

Trophallaxis occurs in termites (Suàrez and Thorne, 2000), ants (Hölldobler and Wilson, 1990; Moreira et al., 2006; Richard and Errard, 2009; Buffin et al., 2011), wasps (Hunt, 2007; Hunt, 2012), and bees (Winston, 1987) (Glossary box). Transfer of liquid can also occur by pseudotrophallaxis, or the “social bucket,” in which liquid moves via capillarity between individuals during contact of one another’s mandibles (Hölldobler and Wilson, 1990). Trophallaxis plays a role in the dynamic processes of colony odor homogenization including recognition cues (Vander Meer and Morel, 1998; Boulay et al., 2000; Lenoir et al., 2001; Chapuisat et al., 2005; Richard and Errard, 2009) or behavior appeasement effects between nestmates in *Leptothorax nylanderi* (Heinze, 1996).

Allogrooming also facilitates colony odor homogenization and is an efficient way to continually update colony odor in response to endogenous and exogenous variation. Self-grooming enables an individual to update its individual odor and maintain chemical perception acuity of the antennae (Böröczky et al., 2013). Cuticular compounds can also be passively transferred by body contact (Vauchot et al., 1998). In many ant species allogrooming distributes cuticular hydrocarbons from the postpharyngeal gland, in which compounds groomed from other individuals have been stored, making this gland an organ that mixes chemical cues (Meskali et al., 1995; Soroker et al., 1998; Lenoir et al., 2001). Hydrocarbon biosynthesis appears to be lower in queens than in workers, but the amount of CHCs in queens’ postpharyngeal glands is higher (Lahav et al., 1998), indicating that queens receive more CHCs than they give during social interactions. Isolated groups of *Camponotus fellah* and *Acromyrmex subterraneus* workers have different postpharyngeal and CHC chemical profiles than those in the colony of origin (Boulay et al., 2000; Richard et al., 2004). Reunification leads to reconvergence of workers’ chemical profiles (Boulay et al., 2004). Both trophallaxis and grooming are important modes for the distribution of colony odor in *C. fellah* (Boulay et al., 2000; Boulay et al., 2004), *Formica polyctena* (Aubert and Richard, 2008), and *Cataglyphis iberica* (Dahbi and Lenoir, 1998b; Dahbi et al., 1999).

The rate of interindividual hydrocarbon transfer is affected by species-specific frequency of both trophallaxis and allogrooming (Soroker et al., 2003, and references therein). In the ponerine ant *Pachycondyla apicalis* workers perform little allogrooming and no trophallaxis, so little hydrocarbon is transferred, but it is sufficient for colony odor homogenization in small colonies (Soroker et al., 1998).

Immune stimulation modulates social interactions

In honeybees, immunochallenged-stimulated workers have different cuticular chemical profiles than untreated individuals of the same colony (Richard et al., 2008; Richard et al., 2012). Individuals with changed profiles elicit more social contact, fewer trophallactic exchanges, and potential segregation of unhealthy individuals (Aubert and Richard, 2008; Richard et al., 2008; Richard et al., 2012). The decrease of social interactions could limit the spread of pathogenic infection. When ants are infected with a generalist insect pathogenic fungus, social interactions between infected and uninfected ants decrease, but cuticular chemical profiles were not altered (Bos et al., 2012).

Chemical regulation of intracolony division of labor

Odor is acquired during a sensitive period

Colony odor recognition may be innate via a recognition template, or it may be acquired during development through processes such as learning or imprinting during a sensitive period (Jaisson, 1987). The sensitive period may occur during development (Isingrini et al., 1985; Cotoneschi et al., 2007) and/or during the first hours after eclosion when it can be learned during interactions with nestmates via transfer of hydrocarbons from adults to callows (recently emerged adults with soft cuticle) during maturation (Hölldobler and Wilson, 1990; Dahbi et al., 1998a; Lenoir et al., 1999; Errard et al., 2006). Larvae of the wasp *Polistes dominula* [*dominulus*] possess a colony-specific CHC pattern that is distinct from that of adults (Cotoneschi et al., 2007). Newly emerged *Polistes* paper wasps learn the colony odor template from the odor of the nest material (Singer and Espelie, 1996; Gamboa, 2004). Newly emerged honeybees have a lower quantity of cuticular lipids than old bees and gradually acquire their colony-specific hydrocarbon profile in part from compounds present in the wax of the honeycomb (Breed et al., 1998; Kather et al., 2011). The low quantity of cuticular lipids facilitates their easy acceptance into foreign colonies (Kather et al., 2011). In the ant *Cataglyphis iberica*, hydrocarbon content in the postpharyngeal glandular secretions of callows increases until the ants reach 10 days of age (Dahbi et al., 1998a), but early isolation of callows decreases the rate of hydrocarbon accumulation in their postpharyngeal glands. Transfer of hydrocarbons from mature workers to previously isolated callows enables those callows to acquire the colony odor and integrate into the colony (Dahbi et al., 1998a). The quantity of hydrocarbons involved in recognition increases as workers get older in *Polistes*, honeybees, ants, and probably other social species. This is the result of both social transfer and the production by individuals.

Chemical signals change with age, caste, and task

Division of labor can be determined by physical castes or age, and it also can be flexible through aggression between nestmates or pheromone effects. Chemical signals related to caste- and task-specific patterns have been shown in termites (Sevala et al., 2000; Liebig et al., 2009; Weil et al., 2009), honeybees (Dani et al., 2004a; Dani et al., 2005; Del Piccolo et al., 2010; Kather et al., 2011), and ants (Greene and Gordon, 2003; Richard et al., 2007a). Termite CHC profiles are caste-specific and could also encode individual-specific information (Sevala et al., 2000), but fertility cues in the higher termite *Zootermopsis nevadensis* include polyunsaturated alkene compounds that do not differ between soldiers, workers, and reproductively inactive secondary reproductives (Liebig et al., 2009).

Honeybee cuticular chemical profiles, especially *n*-alkanes, alkenes, and fatty acids, exhibit a task specific pattern (Kather et al., 2011). Forager honeybees have more *n*-alkanes than newly emerged and nurse workers (Dani et al., 2004a; Del Piccolo et al., 2010; Kather et al., 2011). Young workers interact with bees of all ages with equal frequency, whereas older bees preferentially interact with nestmates of the same age and actively choose social partners (Scholl and Naug, 2011). In the queenless ant *Diacamma ceylonense*, the CHCs of nestmate workers vary in their proportions according to worker age (Cuvillier-Hot et al., 2001). Task-specific cues also regulate task allocation in ant colonies (Wagner et al., 1998; Greene and Gordon, 2003). Experimentally CHC-treated red harvester ants (*Pogonomyrmex barbatus*) recognize an encountered nestmate's task, and this influences the performance by treated workers of particular tasks (Greene and Gordon, 2003). CHC profiles of the ant *Myrmicaria eumenoides* are influenced by Juvenile Hormone III, which accelerates CHC changes and the long-term modulation of task shifting (Lengyel et al., 2007).

Reproductive status, fertility recognition, and queen pheromone

Reproductive and non-reproductive castes often produce specific chemical signatures, and chemical differences between reproductive and non-reproductive castes can communicate individual reproductive status to nestmates (Monnin, 2006; Le Conte and Hefetz, 2008; Peeters and Liebig, 2009), including individual fertility and/or reproductive dominance (Liebig, 2010). CHCs that correlate with reproductive status in social Hymenoptera include *n*-alkanes, methyl-branched alkanes, and alkenes (Monnin, 2006). Reproductive caste identification can be via direct contact to detect non-volatile pheromones such as CHCs, and volatile signals can enable detection of active reproductives at a distance. CHC profiles correlate with ovarian activity of workers in some ants, some halictid bees, and some paper wasps (Denis et al., 2006; Monnin, 2006; Le Conte and Hefetz, 2008; Peeters and Liebig, 2009). Queen-specific hydrocarbon signatures exist in ants, bees, termites, and wasps (Vargo, 1998; Liebig et al., 2000; Liebig et al., 2009; Weil et al., 2009; Liebig, 2010). The presence of the queen elicits variable responses across species in behavior, ovary development, chemical profile, gland secretion, and gene expression. Identified pheromones and their biological function have been studied in the honeybee *Apis mellifera* (reviewed in Le Conte and Hefetz, 2008; Kocher and Grozinger, 2011), the fire ant *Solenopsis invicta* (reviewed in Vargo, 1998), and termites (reviewed in Matsuura, 2012).

Ants

Pheromone characteristics can reveal fertility status in ants (Heinze, 2004; Monnin, 2006; Peeters and Liebig, 2009; Moore and Liebig, 2010). Reproductive queens' primer pheromone production suppresses nestmate fertility and prevents ovary development (Le Conte and Hefetz, 2008). Queen and worker ants can adjust their fecundity in response to brood quantity or presence of other reproductives, thereby enabling adaptive behavioral and physiological responses to changes in colony composition (Holman et al., 2013). Pheromone signals can affect worker reproduction, and variation among workers in ovary activation is best modeled as a threshold response (Barron and Robinson, 2008).

Queens and workers differ significantly in chemical profiles, including CHCs, in *Leptothorax acervorum* and *L. gredleri* (Cuvillier-Hot et al., 2002; Tentschert et al., 2002; Endler et al., 2004; Peeters and Liebig, 2009). Hydrocarbon extracts of reproductive queens of the ant *Myrmecia gulosa* are more attractive to workers than similar extracts from non-reproductive workers (Dietemann et al., 2003). *Formica fusca* queens exhibit different CHC profiles according to their reproductive status, and they receive more care from workers when their fertility increases (Hannonen et al., 2002), which suggests higher worker investment in the most productive queens. In *Lasius niger*, one important hydrocarbon (3-methyl hentriacontane) that is characteristic of the chemical profile of queen-laid eggs could be considered to be a queen pheromone (Holman et al., 2010).

Queen pheromone of the fire ant *Solenopsis invicta* is a mixture of compounds from the postpharyngeal gland and the poison gland (Vargo and Hulsey, 2000) that elicits both primer and releaser responses. It elicits antennating and licking (Vander Meer et al., 1980; Rocca et al., 1983; Glancey et al., 1984), prevents virgin queens from losing their wings and activating their ovaries (Vargo, 1998), and suppresses mated queens' ovary development in polygyne colonies (Fletcher and Blum, 1981). Removal of the active queens affects gene expression in reproductively inactive queens that causes them to shed their wings and activate their ovaries (Wurm et al., 2010). Such changes in reproduction activity imply that chemicals produced by the previous active queens inhibited reproductive development of the other queens and suggests that these chemicals could be the queen pheromone.

Honeybees

In *Apis mellifera*, queen pheromone (Glossary box), affect many aspects of worker behavior and physiology (Le Conte and Hefetz, 2008). The queen mandibular pheromone consists of five major compounds that act in synergy with an additional four compounds (Keeling et al., 2003). Other components have significant effects but remain chemically unidentified (Richard et al., 2007c). Synthetic mixtures of the known queen mandibular pheromone compounds have similar but less pronounced effects than does the presence of a live queen (Slessor et al., 1988). Queen mandibular pheromone elicits diverse behaviors and physiological responses including attraction of workers from a distance, antennating and licking the queen (Slessor et al., 1988), inhibition of workers' ovary development (Butler and Fairey, 1963; Hoover et al., 2003), prevention of the rearing of new queens (Pettis et al., 1995; Melathopoulos et al., 1996), delay the transition from nursing to foraging behavior, and reduction in juvenile hormone secretion (Pankiw et al., 1998). The composition of queen pheromone differs between virgin and mated queens (Slessor et al., 1990; Plettner et al., 1997; Richard et al., 2007c; Le Conte and Hefetz, 2008; Fierro et al., 2011; Richard et al., 2011). The quantity and the relative proportions of all queen mandibular gland compounds affect the number of workers attracted to the live queen or to the extract (Richard et al., 2007c). In one study, demandibulated queens induced workers' retinue behavior and inhibited their ovary development, suggesting the presence of pheromones other than queen mandibular pheromone that affect colony cohesion (Maisonnasse et al., 2010).

Content of the Dufour's gland is qualitatively associated with individual fertility in honeybees. In queens and ovary-developed workers, the Dufour's gland (Fig. 2) profile contains hydrocarbons and esters, whereas the Dufour's gland of sterile workers synthesizes only hydrocarbons (Katzav-Gozansky et al., 1997). The secretion of the queen's Dufour's gland and the mandibular glands are both attractive to workers (Richard et al., 2011), and their chemical composition differs between virgin and mated queens (Le Conte and Hefetz, 2008). Insemination quantity (semen volume) and quality affect chemical profile of both the mandibular gland (Fig. 2) and Dufour's gland, in turn affecting queen-worker interactions (Richard et al., 2007c; Richard et al., 2011). Exposing workers to both queen mandibular pheromone and Dufour's gland extracts simultaneously elicits a stronger inhibition of ovary development than queen mandibular pheromone alone (Katzav-Gozansky et al., 2006). Queen pheromone quality based on both mandibular gland and Dufour's gland chemical composition provides information on a queen's number of mates (Richard et al., 2007c; Richard et al., 2011) and her fertility (Kocher et al., 2008; Kocher et al., 2009). This could be used by workers as an honest signal with positive consequences of genetic diversity on colony fitness (Mattila and Seeley, 2007).

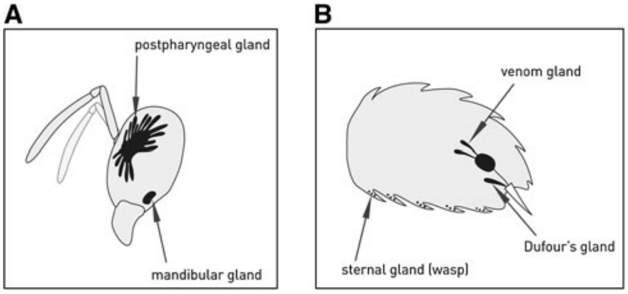

Fig. 2 Generic head (**a**) and abdomen (**b**) of social insect for gland location

Differences in pheromones or diet have larger mean effects on worker ovary activation than genetic factors such as patriline or strain (Backx et al., 2012); moreover, genes for social interactions can be conditionally expressed, depending on the environmental circumstance (Bourke, 2011).

Termites

Termites have both non-volatile and volatile components of queen pheromones. Non-volatile polar compounds of proteinaceous origins are secreted by functional reproductives in the termites *Prorhinotermes simplex, Reticulitermes santonensis*, and *Kalotermes flavicollis* (Hanus et al., 2010). The cuticular hydrocarbon cuticular profile differs between neotenic reproductives and workers in *Cryptotermes secundus* (Weil et al., 2009) and *Zootermopsis nevadensis* (Liebig et al., 2009). In *Z. nevadensis*, four polyunsaturated alkenes are present in significant amounts on reproductives but almost absent in soldiers, workers, and neotenic reproductives with inactive gonads (Liebig et al., 2009). In *Reticulitermes speratus*, queen pheromone consist of volatile compounds which are an ester, n-butyl-n-butyrate, and an alcohol, 2-methyl-1-butanol, and these compounds are not produced by nymphs and workers (Matsuura et al., 2010).

Wasps

CHCs in primitively social wasps provide cues for nestmate discrimination and also discrimination of fertile and non-fertile individuals (Turillazzi et al., 2004). Wasps' Dufour's gland and the abdominal sternal glands (Fig. 2) contain a mixture of lipids similar to the mixture of the cuticular hydrocarbons (reviewed in Bruschini et al., 2010) that could be involved in nestmate recognition in *Polistes* (Dani et al., 1996; Dani et al., 2003). Queens of the primitively eusocial wasp *Ropalidia marginata* appear to maintain reproductive monopoly using secretions from the Dufour's gland that correlate with the state of ovarian activation of queens, suggesting that such compounds may indicate the fecundity of a queen and function as honest signals of fertility (Mitra and Gadagkar, 2011a; Mitra and Gadagkar, 2012). More investigation is needed to determine the possible role of Dufour's gland secretion in the recognition template in Stenogastrinae (Bruschini et al., 2010).

Chemical communication regulates between-worker competition over reproduction

In some social insects, worker sterility can be permanent under queen pheromone and/or behavioral control (Fletcher and Ross, 1985; Dijkstra et al., 2005). In honeybees, some wasps, and some ants, however, orphaned workers and workers that are not exposed to queen pheromone can develop their ovaries and may commence laying eggs that develop into either males or trophic eggs (Winston, 1987; Hölldobler and Wilson, 1990; Dietemann and Peeters, 2000; Dijkstra et al., 2005; Hunt, 2007). Reproductive monopoly over other workers can be subsequently sustained via a queen pheromone (Bhadra et al., 2010). Individual fertility status (queen or egg-laying workers vs. non-egg laying worker) of these species is characterized by different Dufour's gland chemical profiles, which are not colony specific (Mitra et al., 2011b).

Among queenless ant species, the cuticular hydrocarbons of nestmate workers vary with individual reproductive activity in *Diacamma ceylonense* and *Dinoponera quadriceps* (Monnin et al., 1998; Cuvillier-Hot et al., 2001). In *D. quadriceps*, reproductive monopoly of the queen over a pretender (potential egg-laying worker) can result from queen vs. queen pretender interactions in which the pretender is chemically marked by the queen and is then physically punished by non-reproductive workers (Monnin et al., 2002). Dominant, subordinate, and infertile nestmates differ in their relative proportion of the cuticular hydrocarbon 9-hentriacontene (9-C_{31}), and these differences are an honest cue of differences in egg-laying ability between nestmates (Peeters et al., 1999). In the ant *Streblognathus peetersi* the result of agonistic interaction between high-ranking workers determines the future reproductive, and chemical signaling is sufficient to maintain reproductive monopoly when the hierarchy is established (Cuvillier-Hot et al., 2004). In *Gnamptogenys striatula*, reproductive and infertile workers have qualitative and quantitative differences in their CHC profile characterized by five long-chain methyl-alkanes that occur only on the cuticles of unmated and mated egg layers (Lommelen et al., 2006). After queen removal, workers of the ponerine *Pachycondyla goeldi* develop their ovaries, and their CHC profiles also change (11 compounds identified) in an apparent fertility signal (Denis et al., 2006). However, the hydrocarbons in the postpharyngeal gland of *P. goeldi* did not change with the physiological status of workers, thus supporting the hypothesis that the postpharyngeal gland content is involved only in the colony recognition template (Denis et al., 2006).

Reproductive and non-reproductive castes are often morphologically different, and pheromones often play an active role in reproductive/non-reproductive discrimination. In the ant *Myrmecia gulosa*, in which queens and the largest workers are morphologically discrete but queens and the largest workers overlap in size (Dietemann et al., 2002), workers can distinguish queens from fertile workers by means of chemical signatures of CHC (characterized by long-chained hydrocarbons) and the postpharyngeal gland of queens. Queen chemical signature is attractive to workers and can maintain worker sterility without agonistic behaviors (Dietemann et al., 2003, 2005). In the ant *Aphaenogaster cockerelli*, in which queen and worker castes are morphologically distinct, an *n*-alkane provides enough information to reveal the reproductive status of workers (Smith et al., 2009).

Summary and looking ahead

Chemical communication is the most prevalent mode of communication among social insects. It plays fundamental roles in information transfer between and among individuals, nestmate recognition, colony cohesion, behavior, and task regulation. Chemical cues can inform colony members of the presence of reproductive individuals, and in some cases the cues are sufficiently finely tuned to ascertain a reproductive's level of fertility. Cuticular hydrocarbon profiles and secretions of the post-pharyngeal, Dufour's, and mandibular glands are dynamic over time and generally have multiple functions.

Cuticular hydrocarbons (CHCs) are the class of chemicals most widely involved in chemical communication. CHCs are ubiquitous and chemically diverse. Specific CHC compounds usually differ between species. In addition, correlations exist between classes of CHCs or specific CHCs and variables of age, castes, fertility, and health. Qualitative and/or quantitative differences of CHCs can convey information on reproductive status, environmental changes, and characteristics of individuals such as caste and age. In addition to CHCs, compounds such as proteins can also influence individual behaviors.

The relative contributions of heritable, environmentally derived, socially acquired components of colony odor, and individual chemical profile are unknown and pose a challenge for future researchers. The diversity and structural complexity of chemical compounds involved in nestmate and caste recognition may be linked to colony closure by providing enough variation for such discrimination. These chemical compounds change qualitatively and/or quantitatively in response to environmental changes, and environmental effects on colony odor differ from one species to another. At the same time, however, colony and individual odors need to be updated constantly to maintain social functionality and a homogenous colony-specific blend across individuals in the colony. In consequence, colony and individual odors can change over time and also differ among colonies of the same species. A challenge is to discover the chemical cues that social insects use for kin recognition and the genetic encoding of such cues.

Chemical communication often occurs in combination with other sensory channels (Hölldobler, 1999), and the nature and role of chemical communication as part of multimodal communication merits increased attention. New avenues of research could be opened by interdisciplinary research that combines the approaches of physiologists, behavioral ecologists, chemists, ecotoxicologists, and geneticists.

The identification of specific compounds used in nestmate discrimination can be advanced using tools such as gas chromatography coupled with electroantennographic detection (GC/EAD). Columns for gas chromatography with temperatures up to 400 °C can increase the range of compound detection to 60 carbons. In addition, it is now possible to identify hydrocarbon profiles and other surface molecules from living individuals by direct analysis in real-time (DART) mass spectral analysis, thereby enabling individual chemical profiling in parallel with behavioral studies (Yew et al., 2008). The role of proteins in social insect communication can be studied through application of MALDI-TOF (matrix-assisted laser desorption ionization time of flight) mass spectrometry analysis.

Purification of synthesized cuticular hydrocarbons is difficult, and enantiomeric forms and different stereoisometric forms of hydrocarbons are unknown and not taken into account in compound identification. However, insect antennae carry receptors that discriminate between enantiomeric forms, and it has been shown that insect behaviors can be strongly antagonized by the incorrect stereoisomer (Mori, 2007). The role in social insects that molecular variation of this kind may play is currently unknown. Different separation methods exist, and methods used to synthesize several classes of cuticular hydrocarbons are summarized by Millar (2010).

Identification of a pheromone is the essential step for artificially synthesized pheromones to be used in applied research. Synthesized pheromones could be used to attract a large number (mass attraction) of target organisms, or to disturb colony organization to decrease the colony productivity and minimize the species' impact on the environment, or also as a sex attractant during mating season to reduce male mating success and thereby reduce the number of new mated queens in the spread of invasive or undesired species (Baker, 2011).

Chemical communication may be subject to rapid evolutionary change (Symonds and Elgar, 2008), and evolutionary aspects of chemical communication merit attention. For example, queen pheromones that effectively eliminate worker reproduction must have been preceded by less effective pheromones, and those pheromones may have been co-opted from another functional class of pheromones. Genes for social actions can be conditionally expressed, depending on environmental pressure including the behavioral environment (Bourke, 2011; Hunt, 2012). Might evolutionary changes in molecular structure have played a role in increased pheromone effectiveness? What about pheromone blends? The queen pheromone of honeybees is a highly complex mixture of components and has been the focus of a substantial body of research, yet some components of the mixture remain unknown. Queen pheromones exist in other bee species as well as in ants, wasps, and termites. These queen pheromones have been much less studied. Does complexity of chemical structure or chemical blend correspond to complexity of social organization? This and similar evolutionary questions might be addressed via a comparative approach.

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Glossary box

Colony closure: Social insects usually have the ability to distinguish nestmates from non-nestmates, and this can lead to agonistic behaviors directed toward non-nestmates. Non-nestmates can be either allospecific or conspecific. Agonistic behavior directed toward non-nestmates is called colony closure.

Cues and templates: A variety of phenotype components, including cuticular hydrocarbons, behavior, and cell surface proteins can act as cues. By comparing its own cues to a reference set of cues, an individual can define "self" or its individual template. When two individuals encounter one another, they both assess the phenotype cue(s) or label expressed on the other individual and can thereby distinguish nestmates from non-nestmates.

Hydrocarbon: Any of a number of families of compounds, each of which contains only the elements carbon and hydrogen. Cuticular hydrocarbon chemicals (CHCs) are low or non-volatile molecules (mainly those characterized by long chains of >20 carbons) found on insect cuticle that can be divided into ten distinct groups including *n*-alkanes, branched alkanes, alkenes, and alkynes (Fig. 1). Perception of CHCs is usually possible at short distance without individual contact, but contact with the cuticle of another individual enables perception components with low or no volatility.

Queen pheromone: A queen-produced odor or "specific substance" that can act both as releaser and primer pheromone. The queen pheromone composition and gland production vary between species. For example, honeybees' queen mandibular pheromone consists of five major compounds: 9-oxo-(*E*)-2-decenoic acid (ODA); (*R*)-and (*S*)-9-hydroxy-(*E*)-2-decenoic acid (9-HDA); methyl p-hydroxybenzoate (HOB); and 4-hydroxy-3-methoxyphenylethanol (HVA). These compounds act in synergy with an additional four compounds: 8-hydroxyoctanoic acid (8-HOAA); 10-hydroxydecanoic acid (10-HDAA); decanedioic acid (C10:0 DA); and (*E*)-dec-2-enedioic acid (C10:1 DA). The fire ant *Solenopsis invicta* queen pheromone is composed of three main compounds: (E)-6(1-pentenyl)-2H-pyran-2-one; tetrahydro-3,5-dimethyl-6-(1-methylbutyl)2H-pyran-2-one and dihydroactinidiolide.

Lipids: Naturally occurring compounds that are soluble in non-polar solvents. Classes of lipids include waxes, triglycerides, steroids, and prostaglandins.

Pheromone: A single compound or blend of compounds emitted by an actor that changes the physiology (primer pheromone) or behavior (releaser pheromone) of a recipient. Pheromones are exclusively involved in intraspecific communication. In social insects, pheromones include chemical compounds such as cuticular hydrocarbons that do not systematically elicit specific behaviors but are involved in discrimination and recognition of conspecifics or kin. The same pheromone may have multiple functions and can act as both a primer and releaser pheromone. In some cases, the same chemicals can act both as a pheromone (intraspecific) and as an allelochemical (interspecific).

Semiochemicals: Chemical compounds that can be distinguished according to the kind of information transmitted and role in chemical perception and communication. Semiochemicals that play roles among individuals of the same species are called pheromones, and those that play roles in between-species interactions are called allelochemicals.

Trophallaxis: The direct transfer of liquid food from mouth to mouth, or in termites also proctodeum to mouth.

Unicolonial: In most ant species, one nest corresponds to one colony. In some ant species the colony contains several interconnected nests in which all individuals are recognized as colony members. Such colonies are called unicolonial. Invasive unicolonial ants are the most extensive cooperative units in animals, with a few species known to be unicolonial across hundreds of kilometers.

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