Chapter 10
Ontogeny of Nestmate Recognition in Social Hymenoptera

Lisa Signorotti, Rita Cervo and Patrizia d'Ettorre

Abstract The ability to discriminate between friends and foes is a central feature of social life. In social insects, nestmate recognition is mediated by colony specific cuticular hydrocarbons (CHCs) (label) that are perceived by an individual and compared with its neural representation of the colony odour (template). Although numerous advances have been made in understanding the identity, origin and production of recognition cues in social hymenoptera, relatively little is known about the ontogeny of nestmate recognition, and the learning processes that might be involved. It appears that wasps and bees learn the recognition cues required for template formation from their nest/comb odour, while ants learn principally from their nestmates. In general, the referent template is learned during the early stages of adult life, although pre-imaginal learning might play a role. The CHC blend can change over time; cue-exchange among nestmates is therefore needed to reduce chemical variability among individuals and to integrate environmental compounds into the colony odour. As a result of this process, the referent template is updated during life. This relative plasticity of the recognition system can be exploited by insect social parasites to integrate themselves within the host colonies and to fool host workers about their real identity. By studying the chemical integration strategies of social parasites new insights on the ontogeny of nestmate recognition could be acquired. However, further studies are needed to reveal the neural substrates implicated in learning and memory at different stages of social insect life to better understand how and when template formation occurs.

L. Signorotti · P. d'Ettorre (✉)
Laboratory of Experimental and Comparative Ethology (LEEC),
University of Paris 13, Sorbonne Paris Cité, Villetaneuse, France
e-mail: dettorre@leec.univ-paris13.fr

R. Cervo
Department of Biology, University of Firenze,
Sesto Fiorentino, Italy

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Introduction

Recognition plays a central role in parent-offspring interactions, competition, mating and cooperative behaviours such as group defence, brood care, foraging and grooming (e.g., Waldman 1988). Although evidences of recognition abilities in different invertebrate taxa have rapidly accumulated during the past decades (this book), social living certainly generates the most sophisticated and efficient recognition systems. Among invertebrates, insects with eusocial organization represent the most fascinating examples of cooperative group living. Different species of ants, wasps and bees have been traditionally used as model organisms for studying the evolution of cooperative behaviour and recognition systems (Starks 2004). Recognition of group members, i.e., the ability to discriminate between foes and friends, is essential to maintain sociality because it allows altruistic acts to be directed towards related recipients (Hamilton 1987), while excluding competitors and parasites. Differential treatment of relatives and non-relatives, or of different classes of relatives, constitutes kin discrimination. In social insects, colonies typically consist of related individuals, and thus recognition of group membership can act as a proxy for kin recognition (cf. Lenoir et al. 1999). Indeed, no clear evidence of within-colony discrimination based on degree of kin has been provided so far (Boomsma and d'Ettorre 2013).

Here we focus on recognition of group identity (nestmate recognition), the most widespread form of recognition in social insects (d'Ettorre and Lenoir 2010). Group members are usually directly recognized because of traits they express (label) that are perceived by conspecifics and compared with an internal reference (template) stored somewhere in the nervous system. Recognition occurs through the evaluation of how well the label matches the template. This form of identity assessment may be imperfect, leading to acceptance/rejection errors (see Ratnieks 1991), but social insect evolved mechanisms to optimize the system by achieving a unique colony label/template, shared by all colony members, and with minimal overlapping among neighbouring colonies (van Zweden and d'Ettorre 2010). Although we know a great deal about the nature of recognition cues in social insects (which are mainly chemicals, see Fig. 10.1 and this volume Breed et al. and Steiger), we are just starting to understand the perception rules of these nestmate recognition cues and their information processing (Ozaki and Wada-Katsumata 2010; Ozaki and Hefetz 2014). However, relatively little is known about the ontogeny of nestmate recognition, and in particular about the template formation and timing processes. By manipulating individuals' opportunities to interact with conspecifics and/or environment during their life, or part of their life, we may gain a better understanding of the mechanisms underlying nestmate recognition.

Here we present a general overview of the studies that have addressed the ontogeny of nestmate recognition in social hymenoptera, by paying particular attention to the process of template acquisition. Moreover, we will discuss the potential future directions to better understand how recognition information is represented and processed at the peripheral and central level. We begin our overview with highlighting the main general mechanisms that have been proposed to be at the basis of the recognition process.

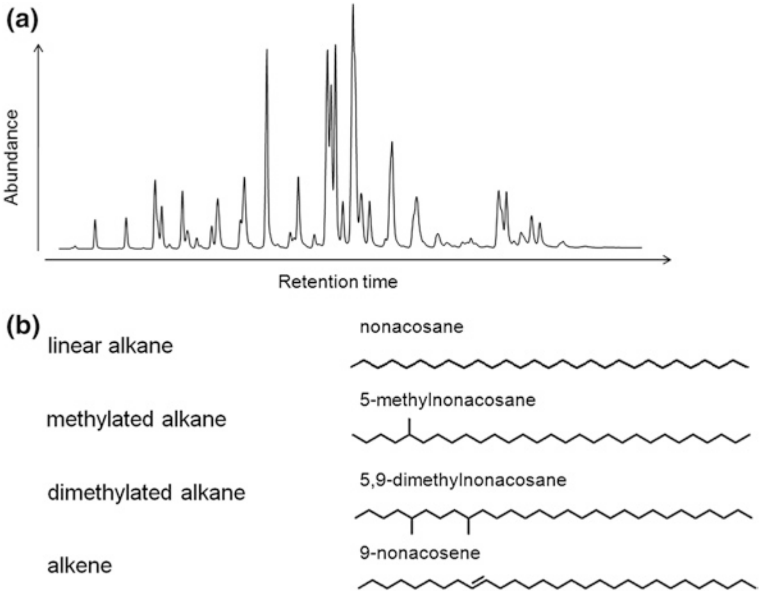

Fig. 10.1 Recognition cues: cuticular hydrocarbons (CHCs) in social insects. **a** Example of chromatogram resulting from CHC analysis by gas chromatography coupled with mass spectrometry (GC-MS). Each *peak* represents one hydrocarbon (or a mixture of few co-eluding hydrocarbons). **b** Examples of the different structural classes of hydrocarbons that can be typically found on the cuticle of social insects. The main structure of hydrocarbons is generally a backbone of carbon atoms with hydrogen atoms attached on empty binding sites. Cuticular hydrocarbons in social insects generally range in size from about 20 to over 40 carbon atoms. CHCs are part of the lipid layer present on the cuticle that protects the insect body against desiccation (Hadley 1994), abrasion and micro-organism infection (Lockey 1988). However, CHCs have assumed a communicative role in several behavioural contexts, especially in social insects where they communicate identity (van Zweden and d'Ettorre 2010; Bruschini et al. 2010). A typical chemical profile of ants, bees and wasps is a complex blend of CHCs, which gives a specific odour to different species and, within a species, to each colony (Singer 1998; Dani 2006; Hefetz 2007; Bruschini et al. 2010; van Zweden and d'Ettorre 2010). There are different classes of hydrocarbons on the cuticle of social insects, although not all of them appear to have the same importance as recognition cues (Châline et al. 2005; Dani 2006; Hefetz 2007; Zweden and d'Ettorre 2010). Methyl-alkanes and alkenes are considered to be relevant nestmate recognition cues (Dani et al. 2001, 2005; Châline et al. 2005; Cervo et al. 2008; Martin et al. 2008; Guerrieri et al. 2009; van Zweden et al. 2010), possibly due to their complex chemical structure compared to linear alkanes, which are more likely involved in water-loss prevention. On the other hand, in the ant *Formica japonica*, all CHC classes appear to be important to achieve discrimination (Akino et al. 2004). The colony odour is generally uniform, but small differences in CHC profiles within the colony can correlated to task (e.g., Greene and Gordon 2003) or caste (Liebig 2010). Moreover, some hydrocarbons, overproduced by queens relative to workers, can act as queen pheromones regulating worker sterility (Peeters et al. 1999; Liebig et al. 2000; Holman et al. 2010, 2013; Monnin 2006; van Oystaeyen et al. 2014)

Recognition Mechanisms

During the last three decades different potential mechanisms underlying recognition of identity have been proposed (reviewed in: d'Ettorre and Lenoir 2010). There is general agreement that these mechanisms are not mutually exclusive or necessary exhaustive, and that their generalization is difficult because ecological constraints and life history trade-offs could affect the recognition mechanism of a particular species (cf. Dreier and d'Ettorre 2009). Generally, recognition could be based on an *indirect* or a *direct* assessment. In the first case recognition is context-based and individuals recognize group members not by their phenotype, but for instance by the specific spatial location where they are encountered. A location, such as the nest site, predictably indicates group membership and all conspecifics encountered therein are recognized as relatives. Alternatively, individuals might recognize group members in a more accurate way, i.e., by *directly* assessing their phenotypic cues through different mechanisms.

Prior association: During social life an individual learns cues from other individuals that are regularly encountered (e.g., group members). These become 'familiar' individuals and in subsequent encounters they will elicit acceptance and/or cooperative behaviour. This type of mechanism requires that each individual must be encountered to become familiar, and thus the recognition process takes place at individual level. There are few examples of individual recognition in social insects, which could be based on this mechanism (Tibbetts 2002; d'Ettorre and Heinze 2005; Dreier et al. 2007; Foubert and Nowbahari 2008). Usually, individual/familiar recognition could work only in small societies, such as those of primitively eusocial wasps (e.g., *Polistes* and Stenogastrinae wasps), in which visual cues are used for the discrimination process (Tibbetts 2002; Baracchi et al. 2013, 2015). On the other hand, ants appear to use chemical cues to achieve individual recognition. For instance, unrelated founding queens of the ant *Pachycondyla villosa* likely use cuticular hydrocarbons (CHCs) to recognize each other individually (d'Ettorre and Heinze 2005).

Phenotype matching: This mechanism allows discrimination of individuals not encountered before. Here, an individual compares the phenotypic cues (label) of the encountered individual with an internal representation (neural template) (Reeve 1989; Crozier and Pamilo 1996; Mateo 2004; d'Ettorre and Lenoir 2010; van Zweden and d'Ettorre 2010). Acceptance/rejection will depend on the similarity/dissimilarity between the template and the label. The template is usually acquired by a learning process. This mechanism is considered as the most used by social insects, being the phenotype (its own or that of nestmates/nest material) a reliable source of cues for recognition of group members (Fig. 10.2).

Recognition alleles (green beard): According to this mechanism, an allele at a single locus (or closely linked genes) should code for three traits linked together: a detectable phenotypic cue (green beard), the ability to recognize this cue and the expression of altruistic behaviour towards individuals with this cue (Hamilton 1964; Dawkins 1976; Holmes and Sherman 1982). In this case, no learning experience is needed.

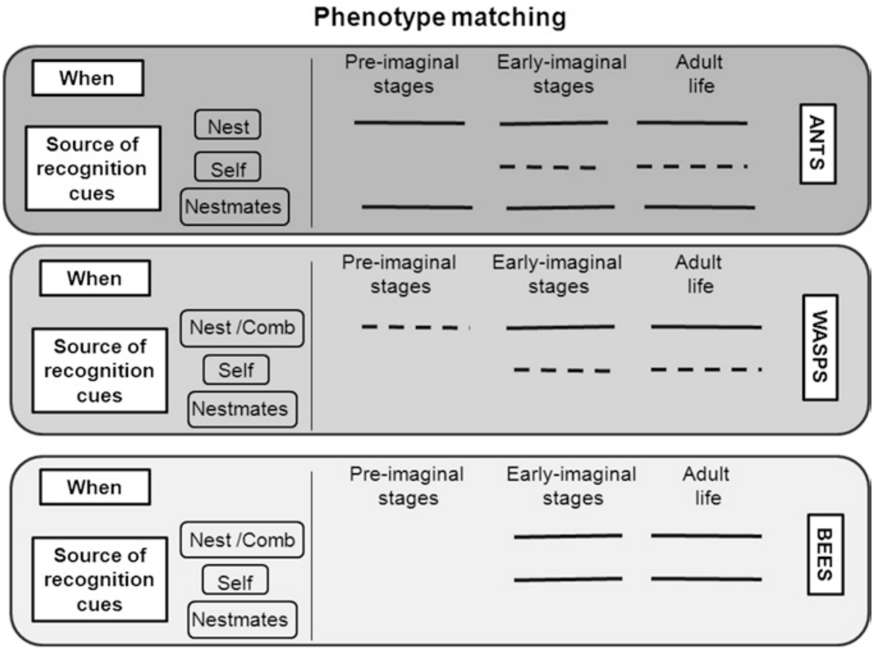

Fig. 10.2 Schematic view of the ontogeny of nestmate recognition ability in ants, wasps and bees according to the phenotype matching model (a possible mechanisms of direct recognition, see text). For each taxonomic group, life stages in which recognition cues can be learned (when) and their source (source of recognition cues) are represented. *Continued lines* indicate factors that have been experimentally shown to play a role in the ontogeny of nestmate recognition, while *dotted lined* indicate factors that are possibly involved

Source of Recognition Cues for Template Formation

In order to build a template, each individual must be in contact with some relevant recognition cues (see Fig. 10.1) during at least part of its life. A parsimonious mechanism for providing all colony members with similar recognition cues could be the exposure to a common source of cues, such as the nest material (Gamboa et al. 1986a). Social wasps of the *Polistes* genus often transfer chemical cues from themselves to the nest material (paper, which easily adsorbs chemical cues) through specific behavioural patterns (Cervo and Turillazzi 1989; Dani et al. 1992; van Hooser et al. 2002). The presence of these cues on the nest surface provides information about colony membership to any new member of the colony (Gamboa et al. 1986a, b). Chemical analyses revealed that the nest material of *Polistes* wasps possesses the same chemical compounds present on the cuticle of the resident wasps (Espelie and Herman 1990; Espelie et al. 1990; Lorenzi 1992; Singer et al. 1992; Cotoneschi et al. 2007). Recognition cues deposition on nest material could thus be important for creating uniformity in the odour label, the so called “Gestalt odour” (cf. Crozier and Dix 1979), and may also contribute to the formation of the referent template. Cues involved in nestmate recognition process are spread within the colony so that nestmates acquire the same or a very similar odour (Crozier and Dix 1979), i.e., a common colony phenotype acting as a uniform identity badge. The *Gestalt* model implies a continuous exchange of recognition cues among nestmates; such mechanism could minimize fluctuation of colonial and individual odours during time due to environmental factors (Carlin and Holldobler 1983; Dahbi and Lenoir 1998; Dahbi et al. 1999; van Zweden et al. 2010). According to the *Gestalt* model, each member of a colony has an odour which is representative of the entire colony. This common odor can thus be used for the formation of the referent template.

There is evidence that some species of *Polistes* wasps learn the referent colony odour (template) from their natal comb early during adult life (Pfennig et al. 1983a, b; Gamboa et al. 1986b; Gamboa 2004; Singer and Espelie 1992). It has been experimentally shown that the presence of the nest material, but not necessarily of nestmates, is important in the ontogeny of nestmate recognition ability in *Polistes fuscatus* wasps (Shellman and Gamboa 1982). *P. fuscatus* gynes (reproductive females) isolated from their natal nest, and gynes exposed only to nestmates after emergence, do not discriminate later between nestmates and unrelated individuals. Similarly, young *Polistes metricus* workers fail to recognize nestmates if they have spent the first four days of their adult life on a comb washed with solvent to remove nest surface compounds (Singer and Espelie 1992). However, in *Polistes dominula* workers, template formation appears to happen in a different way since the absence of nest material (or the presence of alien nest material) during the first four days of adult life does not affect nestmate recognition ability (Signorotti et al. 2014a).

Honeybee guards learn their colony odour from the wax combs in their nest similarly to social wasps (Breed et al. 1995, 1998; d'Ettorre et al. 2006; Couvillon et al. 2007). On the other hand, evidence that nest cues have a recognition function in ants is lacking, although in *Camponotus aethiops* it has been reported that recognition cues can be transferred from one ant to another via the nest soil and this action could affect recognition behaviour (Bos et al. 2011). Ants can leave chemical recognition cues passively on the nest substrate through the contact of their body; however, the resulting deposit is not necessarily colony specific (Lenoir et al. 2009). In ants, template formation appears to be based on cues learned from nestmate workers (e.g., Boulay and Lenoir 2001; Boulay et al. 2003) or from the queen in small colonies (Carlin and Hölldobler 1986). In two *Camponotus* species, there is also evidence that newly eclosed ants familiarize with recognition cues of adult nestmate workers assisting them during eclosion (Morel 1983, 1988). Whatever the source of recognition cues, social insects must be able to identify the common colonial phenotype (e.g., a mix of individual odours to form a single common *Gestalt* odour), perceive it, possibly learn it and form the referent template, on the basis of such phenotype, during a given period of their life.

Timing of Template Formation

Upon emergence, social insects are surrounded by a world of odours that could contain the recognition cues. For the recognition system to be effective, social insects must learn the odour of their specific colony. The role of learning in nestmate recognition is still debated and it remains unclear whether the process of cue learning and template formation is acquired through familiarization during a specific sensitive period (e.g., Jaisson 1987), and when this sensitive period occurs. Indeed, learning could occur at different stages of the insect life (Fig. 10.2).

Early learning: The ability to learn environmental cues during the first moments of life as imago insect (adult) has been investigated since long time. For instance, *Camponotus vagus* and *Formica polyctena* ants develop a preference for a specific habitat as consequence of an early exposure to particular environmental cues, e.g., thyme aroma (Jaisson 1980). In most of the social insect species studied so far, the nestmate recognition cues necessary to build the referent template appear to be learned during the early stages of adult life.

Honeybees learn colonial cues from the wax comb even within an hour after emergence (Breed and Stiller 1992). Studies on the ontogeny of the olfactory nervous system of honeybees have suggested the existence of a critical period, ranging from 3 days before to 4–8 days after emergence, during which the olfactory system appears very flexible in response to environmental changes (Masson et al. 1993). Similarly to honeybees, in *Polistes* wasps early experience after emergence affects nestmate recognition (Gamboa 2004). Gynes of *P. carolina* and *P. fuscatus* isolated at emergence both from their natal nest and their nestmates later failed to recognize nestmates (Pfenning et al. 1983b; Gamboa et al. 1986b). This means that early experience after emergence is crucial for the template development in these species. It has been suggested that the template acquisition in *Polistes* wasps is complete within the first hours after emergence (4 h) (Gamboa 2004); indeed, longer exposure of newly emerged *P. fuscatus* gynes to their natal nest has no effect on discrimination abilities (Pfenning et al. 1983a). *P. fuscatus* wasps are able to remember recognition cues learned during the first hours of adult life up to 20 days later (Pfenning et al. 1983a).

Although numerous evidences suggest that this recognition model is widespread within the genus *Polistes* (including more than 200 species; Carpenter 1996), further investigations are needed since almost all studies were performed on gynes' recognition ability and on limited number of North American species (*P. fuscatus*, Pfenning et al. 1983a; *P. carolina*, Pfenning et al. 1983b; *P. metricus*, Singer and Espelie 1992). Indeed, a recent study conducted on *P. dominula*, an Old World species, suggested the possible implication of other life stages, such as pre-imaginal ones, in which the learning process for the template formation could occur (Signorotti et al. 2014a).

The timing of template formation in ants appears to follow the same general mechanisms as for wasps and bees (Hölldobler and Michener 1980; Jaisson 1991; Lenoir et al. 1999). Early in adult life, each ant learns the colonial cues, which, when encoded as a neural template, serve for colonial membership determination of each encountered individual (Crozier and Pamilo 1996). In *C. vagus* (Morel 1983) and *Camponotus floridanus* (Morel 1988), interactions with older nestmates during the first hours of adult life are necessary to a young worker both to be fully recognized as a nestmate and to develop the ability to recognize nestmates. In some species of ants the recognition of brood can be influenced by the post-eclosion experience (Jaisson 1991). For instance, in *Ectatomma tuberculatum*, an early familiarization of workers with foreign conspecific larvae induces a subsequent preference directed towards them, compared to their own non-familiar larvae (Fénéron and Jaisson 1995). The fact that young workers usually spend the first few days of their life inside the brood chamber may facilitate this learning process (Fénéron and Jaisson 1995).

The use of experimental mixed species groups of ants (rare in nature with the exception of colonies invaded by social parasites) has provided further insight into the timing of template acquisition and its memorization. For instance, newly eclosed workers of *Formica selysi* and *Manica rubida*, reared in artificial mixed colonies, were able to learn allospecific recognition cues, to integrate them into their "colonial template" and to retain them even after one year of separation (Errard 1994a). This implies long-term memory of the template (Errard 1994b), suggesting that the template resides in higher brain centers, such as the mushroom bodies, although, after the long separation, traces of heterospecific hydrocarbons were still present on the cuticle of ants, and could have served as reference (cf. Bos and d'Ettorre 2012).

Pre-imaginal learning: In some ant species, individuals acquire a recognition template for queen recognition (Berton et al. 1991), brood and nestmates recognition (Isingrini et al. 1985; Carlin and Schwartz 1989; Signorotti et al. 2014b) during the pre-imaginal life (i.e., before eclosion). Pre-imaginal olfactory experience affects colony-brood recognition, particularly when experience starts during the first stages of larval development in the ant *Cataglyphis cursor* (Isingrini et al. 1985). Therefore, the first larval instars might be more sensitive to environmental social cues, and/or the total duration of the exposure to the colony odour during pre-imaginal life might affect brood recognition in *C. cursor* adult ants. Similarly, in the ant *Aphaenogaster senilis*, the odour experience during early stages of larval development affects recognition in an adult-adult context (nestmate recognition) (Signorotti et al. 2014b).

Memories from pre-imaginal olfactory experiences can survive after metamorphosis suggesting that the template is probably stored in the higher brain centres. Social insects during their pre-imaginal life are often in contact with recognition cues (nest material/nestmates), therefore the learning process could start during immature stages, when the olfactory system is being formed. Very little is known about structural modifications of social insects' brain during development

(Gronenberg et al. 1996; Farris et al. 1999). The mushroom bodies (higher brain centres) are involved in higher associative functions (learning and memory) and play a key role in the neuronal control of adaptive behavioural modifications and in the processing and storage of chemosensory information (Erber et al. 1980; Menzel 1993; Heisenberg 1994). Certain brain structures, such as the mushroom bodies, develop during larval life (Farris et al. 1999). Indeed, studies on adult mushroom bodies in *Apis mellifera* showed that there are no signs of cell proliferation (neurogenesis) after pupation (Fahrbach et al. 1995; Cayre et al. 1996). Similarly, in the ant *C. floridanus*, neurogenesis is complete in young pupae and no new Kenyon cells (intrinsic neurons of the mushroom bodies), that might contribute to mushroom bodies growth, are produced in adults. Thus, the increase of mushroom bodies' volume in adults is most likely the result of an outgrowth of existing neurons (Gronenberg et al. 1996). The connection between pre-imaginal experience and adult behaviours could be a consequence of the survival of larval/pupal neurons during metamorphosis in the higher brain centres, enabling the persistence of memories formed during pre-imaginal stages in the adult brain (Tully et al. 1994; Lee et al. 1999; Ray 1999).

There are no specific studies on pre-imaginal learning of nestmate recognition cues in social wasps, although some insight comes from studies on facultative social parasites (Lorenzi et al. 2007, 2011; Costanzi et al. 2013). Usually, *Polistes* dominant female performs a typical abdomen stroking behaviour over the nest surface to possibly release chemical cues on the comb, thus spreading her own odour (Dani et al. 1992; van Hooser et al. 2002; Dapporto et al. 2007). Wasp social parasites also perform this behaviour after invading the host nest (Cervo and Turillazzi 1989; Zacchi et al. 1996; Turillazzi et al. 2000). Costanzi et al. (2013) suggested that *P. dominula* workers could memorize the colony odour experienced during pre-imaginal development. They performed an experiment in which natural nests of *P. dominula* wasps were divided into two parts and brood emerged either in the part marked by their genetic mothers or in the part overmarked by *Polistes nimphus* usurpers, in absence of adults. *P. dominula* workers emerged in usurped nests accepted both their usurper and their genetic mother, suggesting that they could have learned their mother's odour during pre-imaginal life. Moreover, worker discrimination abilities were lowest in colonies where the odour changes due to usurpation were largest, indicating a possible process of comparison between the previously learned odour and the new one, i.e., the odour of the parasite (Costanzi et al. 2013). The occurrence of pre-imaginal learning for template formation in *P. dominula* wasps has been recently proposed also by us (Signorotti et al. 2014a). We showed that workers, taken from their natal comb when the natural emergence occurs, displayed correct discrimination abilities at the age of five days, regardless of their olfactory experience during the first four days of adult life. Ecological pressures might have led to the evolution of an advantageous precocious cues learning in *P. dominula* wasps (Signorotti et al. 2014a), a species characterized by high rate of inter- and intraspecific social parasitism (Cervo 2006).

In the Stenogastrinae wasp *Liostenogaster flavolineata*, chemicals on the nest material are scarce since the comb is made with mud; however, in this species an abdominal substance secreted by the Dufour's gland, rich of the same compounds as the wasp cuticle (Cervo et al. 2002; Keegans et al. 1993), is transferred directly on eggs and small larvae (Turillazzi 1985). Although this secretion could contain suitable cues for the acquisition of the recognition template during pre-imaginal stages, behavioural experiments did not confirm the use of this abdominal substance for the formation of the template (Cervo et al. 2002; Turillazzi et al. 2008). Further studies on different species are needed to clarify the possible implication of pre-imaginal learning in template formation.

Template updating during adult life: The occurrence of early and/or pre-imaginal template formation does not exclude a subsequent template updating during adult life. Individual odour and thus colonial odour are dynamic and change over time (Vander Meer and Morel 1998; Lahav et al. 2001; Sledge et al. 2004; Dapporto et al. 2005; van Zweden et al. 2009; Newey et al. 2009; Sturgis and Gordon 2012), suggesting that the template should be updated throughout the adult life for an effective recognition system to be maintained (Liu et al. 1998). We have direct evidences that in several species of Myrmicinae, Formicinae and Ponerinae ants, workers exchange recognition cues (Vienne et al. 1995; Meskali et al. 1995; Soroker et al. 1995, 1998; Dahbi et al. 1999; Boulay et al. 2000; van Zweden et al. 2010) allowing the formation of a unique colonial odour; therefore workers need frequent social contacts with nestmates to maintain an accurate referent template reflecting the current shared odour. In the ant *Camponotus fellah*, the isolation of adult workers for 20 days from the colonial cues can partially erase the workers' template, leading to errors in nestmate recognition due to the impossibility to update the template (Boulay and Lenoir 2001). Social contact during adult life appears to be necessary to maintain a referent template and thus the capacity to discriminate between aliens and nestmates.

Studies with artificial mixed-species groups provided further insight regarding cue-exchange among colony members and the template formation using "collective" nestmate recognition compounds (Stuart 1988; Errard et al. 2006). Ant workers reared in mixed-species groups learn and memorize the homo- and heterospecific chemical cues (i.e., mixed colonial odour) and they incorporate them into their recognition template (Errard 1994b). This template reformation, on the basis of the presence of heterospecific cues into the colonial odour, likely allows the cohabitation of two species in the same nest without displaying interspecific aggression (Vienne et al. 1990; Errard 1994a). Two hypotheses have been suggested (Errard 1994b) to explain the tolerance between two different cohabiting species in mixed colonies: (1) workers could learn two different recognition template (homo- and heterospecific); or (2) workers could compare during each encounter the chemical cues exhibited by the encountered individual with its own chemical profile that possesses heterospecific cues.

Even though no direct evidences for a template updating process are available for social wasps, some information comes again from studies on social parasitism in *Polistes* wasps and indirectly indicates a similar process of updating. For instance, *Polistes biglumis* wasps recognize only the odour of their species in non-parasitized colonies, but learn a template that fits the odour of their own species and that of the social parasite, *Polistes atrimandibularis*, in parasitized colonies (Lorenzi et al. 1999). The process of template updating has also been shown in *Apis mellifera*: guard bees change their referent template after a unidirectional combs transfer from a 'donor' hive to a 'receiver' hive. Couvillon et al. (2007) suggested that the wax comb transfer increases the acceptance of non-nestmates belonging to the 'comb donor' not by changing the odour of the bees, but by updating their colony odour template directly from the wax comb rather than from the contact with conspecifics.

Individual Acquisition of Colonial Cues

Several strong evidences indicate that CHCs are involved in nestmate recognition in social insects (see Fig. 10.1). A particular CHC blend provides the label to each individual, which reveals colony membership. Young individuals produce their own CHCs (genetic components) and later adsorb colonial cues from nestmates or surrounding environment (environmental components) (Vander Meer and Morel 1998; van Zweden et al. 2009), in order to achieve a chemical integration by developing a *Gestalt* odour (Dahbi et al. 1998; Lenoir et al. 1999). Indeed, newly eclosed social insects appear to be "chemically insignificant", i.e., they have only low amounts of CHCs. This allows acceptance of newly eclosed individuals in foreign colonies (Stuart 1992; Lenoir et al. 1999; Breed et al. 2004; Lorenzi et al. 2004; Mitra et al. 2014), since the total quantity of the CHCs on their cuticle is probably below the quantitative perceptual threshold for nestmate recognition (Cini et al. 2009; Ichinoise and Lenoir 2010; Cappa et al. 2014). The acceptance threshold may shift in an adaptive way according to environmental conditions (e.g., Downs and Ratnieks 2000), although how this behavioral shift relates to the underlying perceptual mechanisms is not known.

Newly emerged honeybees gain tolerance inside their colony by presenting the so-called "blank state", i.e., fewer total quantity of chemicals on the cuticular surface than older bees (Breed et al. 2004). *P. fuscatus* adult wasps do not discriminate between nestmate and non-nestmate young gynes (less 48 h-old). Indeed, these young gynes show a slightly quantitatively different chemical profile than 72 h-old gynes, which are instead well recognized (Gamboa et al. 1986b; Panek et al. 2001). It has been shown that *P. fuscatus* and *P. dominula* young wasps change significantly their CHC blend between 24 and 72 h particularly in respect of abundance, relative abundance, and colony specificity of compounds (Panek et al. 2001; Lorenzi et al. 2004). In *P. dominula* wasps, the percentage of certain hydrocarbon classes in the profile decrease significantly during the first 72 h after emergence together with the increase of other hydrocarbon classes. This suggests that certain CHCs may be more important for recognition in younger *Polistes* wasps and/or newborns are recognized by adults as a group with a specific collective profile (Lorenzi et al. 2004).

Likewise, recognition cues of newly emerged bees are consistent across colonies. This suggests that newly emerged bees could have a typical profile that may serve as a cue to older bees for recognizing the newly emerged bee's status (Breed et al. 2004). Laboratory reared *A. mellifera* younger than 12 h are accepted in alien conspecific nests, but acceptance rapidly declines when introduced bees are older (Breed et al. 1988). In many ant species, newly eclosed workers are readily adopted by an unrelated colony (Jaisson 1991). In the ant, *Camponotus pennsylvanicus*, the acceptance of young workers in alien conspecific nests is maximal during the first hours after birth and gradually decreases from 5–8 days after eclosion (Carlin and Hölldobler 1986). Adult *C. cursor* workers are accepted in alien colonies if 4 days old or younger (Nowbahari and Lenoir 1989). However, this is not always the case. In three North American species of *Leptothorax* ants, the transfer of workers 8 months after birth between groups originating from the same colony caused very little aggression (Stuart 1987a). It has also been suggested that young workers might be highly acceptable in alien colonies because they produce an attractive secretion that inhibits the aggression of older workers (Jaisson 1972), but chemical data supporting this hypothesis are still lacking. Callow workers of the slave-making ant *Polyergus rufescens* appear to emit a secretion that is very attractive for *Formica* host workers; they excrete fluid droplets from the tip of the gaster and *Formica* workers actively lick these secretions (proctodeal trophallaxis). This fluid might act as an appeasement signal facilitating the adoption of the slave makers (d'Ettorre and Errard 1999).

Overcoming the Recognition System: Social Parasites

The recognition system as well as its constituent parts (template and label-CHCs) is flexible. As explained above, individual recognition cues can change over time due to environmental factors, and thus the referent template needs to be updated accordingly. This flexibility can be exploited by social parasites to infiltrate the host colonies. The study of parasite strategies to overwhelm the host colony's defence gives the opportunity to better understand the mechanisms at the basis of nestmate recognition process.

Insect social parasites use the social system of other species to exploit the colony worker-force over an extended period of time so that host workers rear parasite reproductives (Wilson 1971). The first problem the parasite has to solve is to be accepted into the host colony as nestmate. One strategy, named "chemical insignificance" (also "blank state"), is to possess a weak quantity of labels on the cuticle that allows the parasite being undetected by the host (Lenoir et al. 2001). For instance, *Acromyrmex insinuator*, social parasite of the leaf-cutting ant *Acromyrmex echinatior*, appears to adopt this strategy: even if they show remarkably different cuticular hydrocarbon profiles compared to the host, they possess a lower total amount of compounds, which are possibly not perceived by the hosts (Lambardi et al. 2007). Such feature, present in most of newly emerged social insects, could represent an effective strategy employed by the parasites to usurp host colonies. An "insignificant status" could allow parasites to initially gain entrance into a host colony, before achieving chemical integration (Lenoir et al. 2001). Two other strategies are possible to reach some degree of chemical congruency with the host: chemical mimicry (in which the parasite actively biosynthesizes the host cues) or camouflage (in which the parasite gets the cues from the host both by passive acquisition, i.e., via contact with host and nest material, and by active acquisition, i.e., via allogrooming and trophallaxis) (Dettner and Liepert 1994; Lenoir et al. 2001). Before usurpation of a *P. dominula* nest, females of the obligate social parasite *Polistes sulcifer* have a chemical profile both simpler and different from that of the host species. A chemical integration process to match the host odour occurs as soon as 90 min after usurpation (Turillazzi et al. 2000). Similarly, chemical analysis of *P. rufescens* ant parasites and its host species revealed that the newly hatched slaver-markers lack a chemical signature at emergence but later develop or acquire a chemical profile matching that of the host species present in the nest (d'Ettorre et al. 2002). Queens of *Polyergus breviceps* and *P. rufescens* fatally attack the resident queen of their *Formica* host species and, during aggressive interactions, cuticular compounds from the host queen are possibly transferred to the parasite queen (Johnson et al. 2001; Lenoir et al. 2001). Parasites often exhibit behaviours involving physical contacts with both the nest surface and their hosts, which may facilitate the mutual transfer of cuticular chemicals (Turillazzi et al. 1990; Lenoir et al. 1992, 2001 Cervo and Dani 1996; Errard et al. 1997; Cervo 2006).

Although the parasite's chemical integration strategies are fundamental during colony invasion, it is possible that chemical host-parasite congruency is not fully achieved at this stage. Therefore, host acceptance could later be improved by modifying the host's referent template. If the host workers, emerging in parasitized colonies, find a good match between the template (referent colonial chemical profile) and the parasite's odour, the parasite will be recognized as nestmate. Indeed, as outlined above, early experiences can be crucially important for the development of the recognition template. Social parasites can exploit early experiences of their hosts by intervening at the right time. For example, slave-making ants during raids usually pillage host pupae so that new host workers will emerge in a colony containing the slave-makers' odour on which they will form the template. This appears to be an effective strategy, indeed, among the ten ant genera displaying interspecific slavery, only one is known to form slave-maker colonies resulting from the mix with adult host workers (Hölldobler and Wilson 1990). Early experience with the odour of parasites in *Temnothorax unifasciatus* ants, the principal host species of *Chalepoxenus muellerianus* and *Myrmoxenus ravouxi* slave-makers, affects nestmate discrimination ability and the successful enslavement by two slave-maker species. However, this is not the case of *Temnothorax parvulus*, a species that in nature is never parasitized. This could be due to a genetically based system of odour discrimination or to an earlier sensitive period for the template formation, namely the pre-imaginal stages (Blatrix and Sermage 2005).

Nestmate discrimination has been shown to be less influenced by social environment during early stages in the ant genus *Camponotus* than in the genus *Formica* (Carlin et al. 1987). Interestingly, no species of *Camponotus* is parasitized by slave-makers, while many *Formica* species are regular hosts to slave-makers. Early behavioural plasticity could thus facilitate the evolution of parasitism. Coevolution occurs between parasites and their hosts (Foitzik et al. 2001; Hare and Alloway 2001) and hosts and parasites species usually show similar cuticular hydrocarbon profiles (Kaib et al. 1993; Brandt et al. 2005), which might facilitate learning of the parasite profile by the host species. Slave-making *P. rufescens* workers are able to adopt a different cuticular signature, both qualitatively and quantitatively, when reared by different *Formica* hosts species as a result of certain plasticity; however, when reared in isolation they show higher chemical similarities with their primary host *F. cunicularia* (d'Ettorre et al. 2002). This similarity could promote the formation of the host template based on the odour of the parasite. In parasitized wasp colonies, the hosts' early experience is also important for the parasite acceptance. Wasp social parasites normally usurp the host nest before emergence of the first generation of workers (Cervo 2006), thus having the opportunity to manipulate the colony odour in absence of workers. This process could allow both the usurpers and their future brood to be recognized as nestmates. Young *P. atrimandibularis* parasites already possess the specific compounds that allow discrimination in *P. biglumis* non-parasitized colonies, however, they are accepted in parasitized nests because of the incorporation of the parasite-specific components in the referent template of the host species (Lorenzi et al. 1999). Parasites could manipulate colony odours by supplementing with their specific compounds the nest material on which the hosts likely form the template (Lorenzi and Bagnères 1996; Lorenzi et al. 1996; Turillazzi et al. 2000).

Social insects' referent template must be flexible to incorporate all the changes of colonial recognition cues due to the environmental factors, for instance to avoid rejection errors (rejection of nestmates). Yet, this plasticity represents a weakness of the recognition system because the parasites can be part of the environmental factors that cause fluctuations of recognition labels (by depositing their own cues and rearing their own brood). Moreover, parasites developing strategies to mask themselves as nestmates, are more easily accepted. In a cost–benefit balance the host should accept the parasites if the costs of correct discrimination exceed the benefits (Zahavi 1977) because recognition errors in which nestmates would be rejected are very costly.

Concluding Remarks and Future Directions

Social insects have been largely used as models for studying detection, perception, learning and memory of recognition cues through the manipulation of their olfactory experiences and their consequent behavioural responses. Workers in a colony gather experience during their whole life, and almost all behavioural responses are fine-tuned through learning (cf. Jeanson and Weidenmüller 2013). Despite this, some fundamental aspects of nestmate recognition system, such as the timing of template formation and its neural location, remain to be clarified.

Self-Referent Phenotype Matching for Recognition

During the last decades, studies on the ontogeny of nestmate recognition have revealed the presence of a sensitive period for learning, during which the template for the colony odour is formed. Social insects appear to learn the crucial recognition cues (heritable, environmental or both) during a sensitive temporal window after birth (early learning) and then use them as referent according to a phenotype matching process. However, they could also use their own phenotypes as referent for nestmate recognition and theoretically this would be the most accurate way to assess relatedness (Mateo 2004). Self-referencing might turn out to be the mechanism of recognition in several contexts that had previously been thought to depend solely on genetic (innate) cues (Jutsum et al. 1979; Getz and Smith 1983; Mintzer and Vinson 1985; Breed et al. 1985; Stuart 1987b). Nevertheless, in the case of social insects, self-referencing could lead to evaluation problems. First, the individuals of a colony usually show differences, although small, in their chemical profile and so every slightly "different" nestmates could be rejected. Indeed, optimal acceptance thresholds theory predicts when an individual should accept or reject in a given encounter, despite incurring the double costs of errors in rejecting true nestmates and accepting alien individuals (Reeve 1989; Johnson et al. 2011). Second, phenotypes used for self-referencing are themselves malleable constructs because CHCs can be subjected to changes due to environmental factors and/or the physiology of the individuals (Wagner et al. 1998; Nielsen et al. 1999; Buczkowski et al. 2005; Provost et al. 2008). Third, in multiple paternity or maternity systems, this process of learning and discrimination could favour nepotistic behaviours and thus it would not be advantageous in ants, bees and wasp societies where such mating systems can be present (Boomsma and d'Ettorre 2013).

Self-referent phenotype matching could be favoured when there is a high risk to learn from foes, such as social parasites. Living in different habitats and under different ecological pressures (e.g., social parasitism) could promote the development of recognition systems with different characteristics. Few studies have reported self-matching in eusocial hymenoptera (Page and Breed 1987; Michener and Smith 1987). Other sources of recognition cues appear to be important in the template acquisition process, such as experience with nest material (Gamboa 2004) or nestmates (Jaisson 1991; Lenoir et al. 1999) during the early stages of life. However, an individual can never be separated from self-cues. Exclusion of self-referencing in *P. fuscatus* gynes was supported by the fact that individuals isolated from eclosion were not able to develop correct recognition ability but were recognized by the adults. This suggests that the recognition cues were present on the young gynes' body but were not used by them to form the referent template (Gamboa et al. 1986b). However, *P. dominula* workers reared in isolation (without nestmates or nest material) for four days from birth are able to perform correct discrimination between nestmates and non-nestmates (Signorotti et al. 2014a), suggesting the possible occurrence of self-referencing for template formation during the first days of life, at least in this species.

Learning cues from self during the first hours of adult life implies that such recognition cues are already present and perceptible. However, most of the studies report that newly eclosed individuals possess low amounts of recognition cues (see above). More studies are needed to investigate whether the amount of CHCs present on young individuals is over the perception thresholds (cf. Cini et al. 2009; Ichinose and Lenoir 2010; Cappa et al. 2014). Evidence for self-referent phenotype matching in honeybees (Getz and Smith 1983, 1986) has been criticized due to the difficulty of entirely eliminating pre-imaginal and social learning. Futures studies manipulating the breeding environment are needed to elucidate whether self-referent phenotype matching occurs in social insects.

Pre-imaginal Learning and the Neural Machinery at the Basis

Despite prenatal olfactory learning has been demonstrated in a wide variety of animals (Hepper and Waldman 1992; Hudson 1993; Schaal et al. 2000; Hepper 2003; Caubet et al. 1992), the possible importance of learning during immature life in the ontogeny of recognition abilities and social memories has been neglected so far in social insects. The ability of individuals to learn prenatally may be of particular importance in the development of social recognition by ensuring that individuals learn about genetically related conspecifics (Hepper 1987; Robinson and Smotherman 1991). There is evidence that pre-imaginal experience affects recognition abilities in Myrmicinae (Signorotti et al. 2014b) and Formicinae (Isingrini et al. 1985; Carlin and Schwartz 1989) ants. This means that some important information could be processed during the larval stages, retained across the pupal stage, and then integrated into the adult nervous system. Adults and larvae of holometabolous insects are morphologically divergent, reflecting their different lifestyles. Metamorphosis could imply dramatic changes in larval organization, including replacement of the integument and many other tissues, and histolysis of almost all muscles. However, radical changes in neuronal design from the larval to the adult system is not very likely, given that the metamorphosis of the nervous system is largely parsimonious (Tissot and Stocker 2000). Persistence of neurons is not only economic in terms of minimal numbers of neurons to be formed, but might also be crucial for complex metamorphic processes such as axon guidance or memory retention (Tissot and Stocker 2000). Most of the studies on larval chemosensory system have been conducted using *Drosophila* as model (Singh and Singh 1984; Ito and Hotta 1992; Heimbeck et al. 1999; Lee et al. 1999). The larval olfactory circuit of *Drosophila* shows a strong overall similarity to the adult design, but it is organized in a numerically much reduced and almost completely non-redundant way (Ramaekers et al. 2005; Python and Stocker 2002). Young individual neurons could possess integrative capacities as high as that of their adult counterparts; indeed, larvae already exhibit appetitive olfactory learning that relies on a small subset of embryonic-born Kenyon cells (Cobb and Domain 2000; Pauls et al. 2010). Very little is known about the development of larval chemosensory system in social insects.

To elucidate unexplored phenomena, such as pre-imaginal learning, it is essential to determine the actual cognitive load of this particular process and identify how many neurons, connections, and sequential stages of information processing are required to form stable memories until the adult age. From the experimental point of view, one of the major problems in studying pre-imaginal learning lays in the difficulty to assess the behaviour of individuals just after emergence (in most cases they will not respond because too young), and thus there might always be a component due to early learning during the first phase of adult life. Moreover, it could be hard to differentiate between pre-imaginal and self-referent learning if some recognition cues are transferred from the pupal to the adult stage (see Corbet 1985 for discussion on the “chemical legacy hypothesis”). Although recognition cue exchange is possible between adult-adult or adult-nest material (Soroker et al. 1994, 2003; Dahbi et al. 1999; Breed et al. 1995), we do not know whether the larval-adult cue-transfer is possible in social insects.

Regardless of the cue-source, sensitive periods are reflected in behaviour but they are actually a property of neural circuits: behavioural responses are not possible without the processing of the information in the neural machinery. We think that much needs to be learned about nervous system development, neuronal plasticity and the adaptation by studying the brain of social insects. For instance, there are no studies on olfactory organ and receptor cells in ants, bees or wasp larvae.

The Neural Substrates for Nestmate Recognition

Memory has an important role in the discrimination process, both in pre-imaginal and early learning. Several species of ants and paper wasps show long-term memory of nestmate cues, even after overwintering, and there are some evidences that their templates, formed through an imprinting-like process, are maintained over time (Ross and Gamboa 1981; Pfennig et al. 1983b; Gamboa 1988; Jaisson 1991; Errard 1994b; but see Dapporto et al. 2004). However, some characteristics of the recognition system (see above) suggest that the template is not as stable as previously thought and that it could be reformed during life (template updating). It is largely accepted that the neural substrates of memories are parts of the higher brain centers such as mushroom bodies and/or lateral horn (d'Ettorre and Lenoir 2010; Bos and d'Ettorre 2012), but how do they contribute to the behavioural plasticity is less well understood (Heisenberg 1998).

Template updating may result from the formation of new memories each time the referent colonial odour changes or from sensory adaptation or habituation processes, thus the template could be decentralized. In *Camponotus japonicus* ants, the olfactory *sensilla* have been proposed as processing organs for nestmate recognition cues (Ozaki et al. 2005). These *sensilla* show a physiological activity only if exposed to CHCs of non-nestmates, suggesting sensory adaptation as proximate mechanism of nestmate recognition due to the permanent exposure to the colonial odours. However, there are neurophysiological evidences that, for instance in *C. floridanus* ants, colony odours from both nestmates and non-nestmates are perceived and produce a response in the antennal lobes, the first-order integration centers of the central nervous system, contradicting the sensory adaptation hypothesis for nestmate recognition (Brandstaetter et al. 2011). The template reformation is a relatively slow process, taking several hours (Leonhardt et al. 2007; Stroeymeyt et al. 2010) while sensory adaptation at antennal level is much faster. Template adjustment could probably not reverse immediately the own colonial template previously learned (Leonhardt et al. 2007; Harano and Sasaki 2006). During the early phase of template renewal, old memories could be useful to avoid recognition errors while the colony odour is changing. Even if memory is costly (Guerrieri et al. 2011), it could play a key role in the discrimination process. Habituation and/or sensory adaptation, being less costly, could partly replace the use of long-term memory to discriminate nestmates and could be useful during template updating, but the use of memories from the pre-imaginal and/or early adult stages of life remain a key feature in the ontogeny of recognition. A fundamental debate that continues to the present is whether specific mechanisms underlie sensitive periods for learning recognition cues, or whether the presence of sensitive periods is a natural consequence of functional brain development. Future integrated studies are needed to establish how social insect brains develop to allow the complex communication signals to be generated and processed, enlightening certain unclear phenomena such as pre-imaginal learning.

References

Akino T, Yamamura K, Wakamura S, Yamaoka R (2004) Direct behavioral evidence for hydrocarbons as nestmate recognition cues in *Formica japonica* (Hymenoptera: Formicidae). Appl Entomol Zool 39:381–387

Baracchi D, Petrocelli I, Cusseau G, Pizzocaro L, Teseo S, Turillazzi S (2013) Facial markings in the hover wasps: quality signals and familiar recognition cues in two species of Stenogastrinae. Anim Behav 85(1):203–212

Baracchi D, Petrocelli I, Chittka L, Ricciardi G, Turillazzi S (2015) Speed and accuracy in nestmate recognition: a hover wasp prioritizes face recognition over colony odour cues to minimize intrusion by outsiders. Proc R Soc B 282(1802):2014–2750

Blatrix R, Sermage C (2005) Role of early experience in ant enslavement: a comparative analysis of a host and a non-host species. Fron Zool 2(1):13

Berton F, Lenoir A, Nowbahari E, Barreau S (1991) Ontogeny of queen attraction to workers in the ant *Cataglyphis cursor* (Hymenoptera: Formicidae). Insect Soc 38:293–305

Boomsma JJ, d'Ettorre P (2013) Nice to kin and nasty to non-kin: revisiting Hamilton's early insights on eusociality. Biol Lett 9(6):20130444

Bos N, d'Ettorre P (2012) Recognition of social identity in ants. Front Psychol 3:83

Bos N, Grinsted L, Holman L (2011) Wax on, wax off: nest soil facilitates in direct transfer of recognition cues between ant nestmates. PLoSONE 6:e19435

Boulay R, Lenoir A (2001) Social isolation of mature workers affects nestmate recognition in the ant *Camponotus fellah*. Behav Process 55:67–73

Boulay R, Hefetz H, Soroker V, Lenoir A (2000) *Camponotus fellah* colony integration: worker individuality necessitates frequent hydrocarbon exchanges. Anim Behav 59:1127–1133

Boulay R, Katzav-Gozansky T, Vander Meer RK, Hefetz A (2003) Colony insularity through queen control on worker social motivation in ants. Proc R Soc Lond B 270:971–977

Brandstaetter AS, Rössler W, Kleineidam CJ (2011) Friends and foes from an ant brain's point of view—neuronal correlates of colony odors in a social insect. PLoS ONE 6(6):e21383

Brandt M, Heinze J, Schmitt T, Foitzik S (2005) A chemical level in the coevolutionary arms race between an ant social parasite and its hosts. J Evol Biol 18:576–586

Breed MD, Stiller TM (1992) Honey bee, *Apis mellifera*, nestmate discrimination: hydrocarbons effects and the evolutionary implications of comb choice. Anim Behav 43:875–883

Breed MD, Butler L, Stiller TM (1985) Kin discrimination by workers in genetically mixed groups. Proc Natl Acad Sci USA 82:3058–3061

Breed MD, Stiller TM, Moor MJ (1988) The ontogeny of kin discrimination cues in the honey bee, *Apis mellifera*. Behav Genet 18(4):439–448

Breed MD, Garry MF, Pearce AN, Bjostad L, Hibbard B, Page RE (1995) The role of wax comb in honeybee nestmate recognition: genetic effects on comb discrimination, acquisition of comb cues by bees, and passage of cues among individuals. Anim Behav 50:489–496

Breed MD, Leger EA, Pearce AN, Wang YJ (1998) Comb wax effects on the ontogeny of honey bee nestmate recognition. Anim Behav 55:13–20

Breed MD, Perry S, Bjostad LB (2004) Testing the blank state hypothesis: why honey bee colonies accept young bees Insect Soc 51:12–16

Bruschini C, Cervo R, Turillazzi S (2010) Pheromones in social wasps. In: Litwack G (ed) Vitamins and hormones, vol 83. Academic Press, Burlington, pp 447–492

Buczkowski G, Kumar R, Suib SL, Silverman J (2005) Diet-related modification of cuticular hydrocarbon profiles of the Argentine ant, *Linepithema humile*, diminishes intercolony aggression. J Chem Ecol 31: 829–843

Cappa F, Bruschini C, Cipollini M, Pieraccini G, Cervo R (2014) Sensing the intruder: a quantitative threshold for recognition cues perception in honeybees. Naturwiss 101:149–152

Carlin N, Hölldobler B (1983) Nestmate and kin recognition in interspecific mixed colonies of ants. Science 222:1027–1029

Carlin N, Hölldobler B (1986) The kin recognition system of carpenter ants (*Camponotus* spp.). I. Hierarchical cues in small colonies. Behav Ecol Sociobiol 19:123–134

Carlin NF, Schwartz PH (1989) Pre-imaginal experience and nestmate brood recognition in the carpenter ant, *Camponotus floridanus*. Anim Behav 38:89–95

Carlin NF, Halpern R, Hölldobler B, Schwartz P (1987) Early learning and the recognition of conspecific cocoons by carpenter ants (*Camponotus* spp.). Ethology 75:306–316

Carpenter JM (1996) Phylogeny and biogeography. In: Turillazzi S, West-Eberhard MJ (eds) Natural history and evolution of paper wasps. Oxford University Press, Oxford, pp 18–57

Caubet Y, Jaisson P, Lenoir A (1992) Preimaginal induction of adult behaviour in insects. Q J Exp Psychol B 44B:165–178

Cayre M, Strambi C, Charpin P, Augier R, Meyer MR, Edwards JS, Strambi A (1996) Neurogenesis in adult insect mushroom bodies. J Comp Neurol 371:300–331

Cervo R (2006) *Polistes* wasps and their social parasites: an overview. Ann Zool Fenn 43:550–563

Cervo R, Dani FR (1996) Social parasitism and its evolution in *Polistes*. In: Turillazzi S, West Eberhard MJ (eds) Natural history and the evolution of paper wasps. Oxford University Press, Oxford, pp 98–112

Cervo R, Turillazzi S (1989) Nest exchange experiments in *Polistes gallicus* (L.) (Hymenoptera Vespidae). Ethol Ecol Evol 1(2): 185–193

Cervo R, Dani FR, Zanetti P, Massolo A, Turillazzi S (2002) Chemical nestmate recognition in a stenogastrine wasp, *Liostenogaster flavolineata* (Hymenoptera: Vespidae). Ethol Ecol Evol 14:351–363

Cervo R, Dani FR, Cotoneschi C, Scala C, Lotti I, Strassmann JE, Queller DC, Turillazzi S (2008) Why are larvae of the social parasite wasp *Polistes sulcifer* not removed from the host nest? Behav Ecol Sociobiol 62(8):1319–1331

Châline N, Sandoz JC, Martin SJ, Ratnieks FLW, Jones GR (2005) Learning and discrimination of individual cuticular hydrocarbons by honeybees (*Apis mellifera*). Chem Senses 30:327–335

Cini A, Gioli L, Cervo R (2009) A quantitative threshold for nestmate recognition in a paper social wasp. Biol Lett 5:459–461

Cobb M, Domain I (2000) Olfactory learning in individually assayed *Drosophila* larvae. Proc R Soc Lond B 267:2119–2125

Corbet SA (1985) Insect Chemosensory Responses—a chemical legacy hypothesis. Ecol Entomol 10(2):143–153

Costanzi E, Bagnères AG, Lorenzi MC (2013) Changes in the hydrocarbon proportions of colony odor and their consequences on nestmate recognition in social wasps. PLoS ONE 8(5):e65107

Cotoneschi C, Dani FR, Cervo R, Sledge MF, Turillazzi S (2007) *Polistes dominulus* (Hymenoptera: Vespidae) larvae have their own chemical signatures. J Insect Physiol 53:954–963

Couvillon MJ, Caple JP, Endsor SL, Kärcher M, Russell TE, Storey DE, Ratnieks FLW (2007) Nest-mate recognition template of guard honeybees (*Apis mellifera)* is modified by wax comb transfer. Biol Lett 3:228–230

Crozier RH, Dix MW (1979) Analysis of two genetic models for the innate components of colony odor in social Hymenoptera. Behav Ecol Sociobiol 47:217–224

Crozier RH, Pamilo P (1996) Evolution of social insect colonies. Oxford University Press, Oxford

Dahbi A, Lenoir A (1998) Nest separation and the dynamics of the Gestalt odor in the polydomous ant *Cataglyphis iberica* (Hymenoptera, Formicidae). Behav Ecol Sociobiol 42:349–355

Dahbi A, Cerdá X, Lenoir A (1998) Ontogeny of colonial hydrocarbon label in callow workers of the ant *Cataglyphis iberica*. Comptes Rendus de l'Académie des Sciences—Series III—Sciences de la Vie 321:395–402

Dahbi A, Hefetz A, Cerdá X, Lenoir A (1999) Trophallaxis mediates uniformity of colony odor in *Cataglyphis iberica* ants (Hymenoptera, Formicidae). J Insect Behav 12:559–567

Dani FR (2006) Cuticular lipids as semiochemicals in paper wasps and other social insects. Ann Zool Fenn 43:500–514

Dani FR, Cervo R, Turillazzi S (1992) Abdomen stroking behaviour and its possible functions in *Polistes dominulus* (Christ) (Hymenoptera Vespidae). Behav Process 28:51–58

Dani FR, Jones GR, Destri S, Spencer SH, Turillazzi S (2001) Deciphering the recognition signature within the cuticular chemical profile of paper wasps. Anim Behav 62:165–171

Dani FR, Jones GR, Corsi S, Beard R, Pradella D, Turillazzi S (2005) Nestmate recognition cues in the honey bee: differential importance of cuticular alkanes and alkenes. Chem Senses 30:477–489

Dapporto L, Pansolli C, Turillazzi S (2004) Hibernation clustering and its consequences for associative nest foundation in *Polistes dominulus* (Hymenoptera Vespidae). Behav Ecol Sociobiol 56:315–321

Dapporto L, Sledge MF, Turillazzi S (2005) Dynamics of cuticular chemical profiles of *Polistes dominulus* workers in orphaned nests. J Insect Physiol 51:969–973

Dapporto L, Santini A, Dani FR, Turillazzi S (2007) Workers of a *Polistes* paper wasp detect the presence of their queen by chemical cues. Chem Senses 32(8):795–802

Dawkins R (1976) The selfish gene. Oxford University Press, NewYork

Downs SG, Ratnieks FLW (2000) Adaptive shifts in honey bee (*Apis mellifera* L.) guarding behavior support predictions of the acceptance threshold model. Behav Ecol 9:326–333

Dettner K, Liepert C (1994) Chemical mimicry and camouflage. Ann Rev Entomol 39(1):129–154

d'Ettorre P, Errard C (1999) Trophallaxie proctodéale chez la fourmi esclavagiste *Polyergus rufescens*. Actes Coll Insectes Soc 12:61–64

d'Ettorre P, Heinze J (2005) Individual recognition in ant queens. Curr Biol 15:2170–2174

d'Ettorre P, Lenoir A (2010) Nestmate recognition. In: Lach L, Parr CL, Abbott KL (eds) Ant ecology. Oxford University Press, Oxford, pp 194–209

d'Ettorre P, Mondy N, Lenoir A, Errard C (2002) Blending in with the crowd: social parasites integrate into their host colonies using a flexible chemical signature. Proc R Soc Lond B 269:1911–1918

d'Ettorre P, Wenseleers T, Dawson J, Hutchinson S, Boswell T, Ratnieks FLW (2006) Wax combs mediate nestmate recognition by guard honey bees. Anim Behav 71:773–779

Dreier S, d'Ettorre P (2009) Social context predicts recognition systems in ant queens. J Evol Biol 22(3):644–649

Dreier S, van Zweden JS, d'Ettorre P (2007) Long term memory of individual identity in ant queens. Biol Lett 17:459–462

Erber J, Masuhr TH, Menzel R (1980) Localization of short-term memory in the brain of the bee, *Apis mellifera*. Behav Neural Biol 62:259–263

Errard C (1994a) Development of interspecific recognition behavior in the ants *Manica rubida* and *Formica selysi* (Hymenoptera: Formicidae) reared in mixed-species groups. J Insect Behav 7:83–99

Errard C (1994b) Long-term memory involved in nestmate recognition in ants. Anim Behav 48:263–271

Errard C, Fresneau D, Heinze J, Francoeur A, Lenoir A (1997) Social organization in the guest-ant *Formicoxenus provancheri*. Ethology 103:149–159

Errard C, Hefetz A, Jaisson P (2006) Social discrimination tuning in ants: template formation and chemical similarity. Behav Ecol Sociobiol 59(3):353–363

Espelie KE, Hermann HR (1990) Surface lipid of the social wasp *Polistes annularis* (L.) and its nest and nest pedicel. J Chem Ecol 16:1841–1852

Espelie KE, Wenzel JW, Chang G (1990) Surface lipids of social wasp *Polistes metricus* say and its nest and pedicel and their relation to nestmate recognition. J Chem Ecol 16:2229–2241

Fahrbach SE, Strande JL, Robinson GE (1995) Neurogenesis is absent in the brains of adult honey bees and does not explain behavioural neuroplasticity. Neurosci Lett 197:145–148

Farris SM, Robinson GE, Davis RL, Fahrbach SE (1999) Larval and pupal development of the mushroom bodies in the honey bee. Apis mellifera J Comp Neurol 414:97–113

Fénéron R, Jaisson P (1995) Ontogeny of nestmate brood recognition in a primitive ant, *Ectatomma tubercalutum* Olivier (Ponerinae). Anim Behav 50(1):9–14

Foitzik S, DeHeer CJ, Hunjan DN, Herbers JM (2001) Coevolution in host-parasite systems: behavioural strategies of slave-making ants and their hosts. Proc R Soc Lond B 268:1139–1146

Foubert E, Nowbahari E (2008) Memory span for heterospecific individuals'odors in an ant, *Cataglyphis cursor*. Learn Behav 36:319–326

Gamboa GJ (1988) Sister, aunt-niece, and cousin recognition by social wasps. Behav Genet 18:409–423

Gamboa GJ (2004) Kin recognition in eusocial wasps. Ann Zool Fennici 41:789–808

Gamboa GJ, Reeve HK, Pfennig DW (1986a) The evolution and ontogeny of nestmate recognition in social wasps. A Rev Entomol 31:431–454

Gamboa GJ, Reeve HK, Ferguson I, Wacker TL (1986b) Nestmate recognition in social wasps: the origin and acquisition of recognition odours. Anim Behav 34:685–695

Getz WM, Smith KB (1983) Genetic kin recognition: honey bees discriminate between full and half sisters. Nature 302:147–148

Getz WM, Smith KB (1986) Honey bee kin recognition: learning self and nestmate phenotypes. Anim Behav 34:1617–1626

Greene MJ, Gordon DM (2003) Social insects cuticular hydrocarbons inform task decisions. Nature 423:32

Gronenberg W, Heeren S, Hölldobler B (1996) Age-dependent and task-related morphological changes in the brain and the mushroom bodies of the ant *Camponotus floridanus*. J Exp Biol 199:2011–2019

Guerrieri FJ, Nehring V, Jørgensen CG, Nielsen J, Galizia CG, d'Ettorre P (2009) Ants recognize foes and not friends. Proc R Soc B 276:2461–2468

Guerrieri FJ, d'Ettorre P, Devaud JM, Giurfa M (2011) Long- term olfactory memories are stabilised via protein synthesis in *Camponotus fellah* ants. J Exp Biol 214:3300–3304

Hadley NF (1994) Water relations of terrestrial arthropods. Academic Press, San Diego

Hamilton WD (1964) The genetical evolution of social behaviour. J Theor Biol 7:1–50

Hamilton WD (1987) Discrimination nepotism: expectable, common, overlooked. In: Fletcher DJC, Michener CD (eds) Kin recognition in animals. Wiley, New York, pp 417–437

Harano K, Sasaki M (2006) Renewal process of nestmate recognition template in European honeybee *Apis mellifera* L. (Hymenoptera: Apidae). Appl Entomol Zool 41(2): 325–330

Hare JF, Alloway TM (2001) Prudent *Protomognathus* and despotic *Leptothorax duloticus*: differential costs of ant slavery. Proc Natl Acad Sci USA 98:12093–12096

Hefetz A (2007) The evolution of hydrocarbon pheromone parsimony in ants (Hymenoptera: Formicidae)—interplay of colony odor uniformity and odor idiosyncrasy: a review. Myrmecol News 10:59–68

Heimbeck G, Bugnon V, Gendre N, Häberlin C, Stocker RF (1999) Smell and taste perception in *D. melanogaster* larva: toxin expression studies in chemosensory neurons. J Neurosci 19:6599–6609

Heisenberg M (1994) Central brain function in insects: genetic studies on the mushroom bodies and central complex in *Drosophila*. Forts Zool 39:30–39

Heisenberg M (1998) What do the mushroom bodies do for the insect brain? Intro Learn Mem 5(1):1–10

Hepper PG (1987) The amniotic fluid: an important priming role in kin recognition. Anim Behav 35(5):1343–1346

Hepper PG, Waldman B (1992) Embryonic olfactory learning in frogs. Q J Exp Psychol B 44(3–4): 179–197

Hepper PG (2003) Prenatal psychological and behavioural development. In: Valsiner J, Connolly KJ (eds) The handbook of developmental psychology. Sage, London, pp 91–114

Hölldobler B, Michener CD (1980) Mechanisms of identification and discrimination in social Hymenoptera. In: Markl H (ed) Evolution of social behavior: hypotheses and empirical tests. VC, Weinheim, pp 35–58

Hölldobler B, Wilson EO (1990) The ants. Belknap Press, Cambridge, p 732

Holman L, Jørgensen CG, Nielsen J, d'Ettorre P (2010) Identification of an ant queen pheromone regulating worker sterility. Proc R Soc B 277(1701):3793–3800

Holman L, Leroy C, Jørgensen C, Nielsen J, d'Ettorre P (2013) Are queen ants inhibited by their own pheromone? Regulation of productivity via negative feedback. Behav Ecol 24(2):380–385

Holmes WG, Sherman PW (1982) The ontogeny of kin recognition in two species of ground squirrels. Am Zool 22:491–517

Hudson R (1993) Olfactory imprinting. Current Opin Neurobiol 3(4):548–552

Ichinose K, Lenoir A (2010) Hydrocarbons detection levels in ants. Insect Soc 57:453–455

Isingrini M, Lenoir A, Jaisson P (1985) Preimaginal learning as a basis of colony brood recognition in the ant *Cataglyphis cursor*. Proc Nat Acad Sci, USA 82:8545–8547

Ito K, Hotta Y (1992) Proliferation pattern of postembryonic neuroblasts in the brain of *Drosophila melanogaster*. Dev Biol 149:134–148

Jaisson P (1972) Mise en évidence d'une phéromone d'attractivité produite la jeune ouvrière *Formica* (Hymenoptera : Formicidae). C R Acad Sci Paris Ser D 274:429–432

Jaisson P (1980) Environmental preference induced experimentally in ants (Hymenoptera: Formicidae). Nature 286:388–389

Jaisson P (1987) The construction of fellowship between nestmates in social hymenoptera. In: Pasteels JM, Deneubourg JL (eds) Experientia supplementum 54. From individual to collective behaviour in social insects. Birkhauser Verlag, Basel, pp 313–331

Jaisson P (1991) Kinship and fellowship in ants and social wasps. In. Hepper PG (ed) Kin recognition. Cambridge University Press, Cambridge, pp 60–93

Jeanson R, Weidenmüller A (2013) Interindividual variability in social insects–proximate causes and ultimate consequences. Biol Rev, pp 671–687

Johnson CA, Vander Meer RK, Lavine B (2001) Changes in the cuticular hydrocarbon profile of the slave-maker ant queen, *Polyergus breviceps* Emery, after killing a *Formica* host queen (Hymenoptera: Formicidae). J Chem Ecol 27(9):1787–1804

Johnson BR, van Wilgenburg E, Tsutsui ND (2011) Nestmate recognition in social insects: overcoming physiological constraints with collective decision making. Behav Ecol Sociobiol 65(5):935–944

Jutsum AR, Saunders TS, Cherrett JM (1979) Intraspecific aggression in the leaf-cutting ant *Acromyrmex octospinosus*. Anim Behav 27:839–844

Kaib M, Heinze J, Ortius D (1993) Cuticular hydrocarbons profiles in the slave-making ant *Harpogoxenus sublaevis* and its hosts. Naturwissenschaften 80:281–285

Keegans SJ, Morgan ED, Turillazzi S, Jackson BD, Billen J (1993) The dufour gland and the secretion placed on eggs of two species of social wasps, *Liostenogaster flavolineata* and *Parischnogaster jacobsoni* (Vespidae: Stenogastrinae). J Chem Ecol 19:279–290

Lahav S, Soroker V, VanderMeer RK, Hefetz A (2001) Segregation of colony odor in the desert ant *Cataglyphis niger*. J Chem Ecol 27:927–943

Lambardi D, Dani FR, Turillazzi S, Boomsma JJ (2007) Chemical mimicry in an incipient leaf-cutting ant social parasite. Behav Ecol Sociobiol 61(6):843–851

Lee T, Lee A, Luo L (1999) Development of the *Drosophila* mushroom bodies: sequential generation of three distinct types of neurons from a neuroblast. Development 126:4065–4076

Lenoir A, Errard C, Francoeur A, Loiselle R (1992) Relations entre la fourmi parasite *Formicoxenus provancheri* et sur hôte *Myrmica incompleta*. Données biologiques et éthologiques (Hym. Formicidae). Insect Soc 39:81–97

Lenoir A, Fresneau D, Errard C, Hefetz A (1999) Individuality and colonial identity in ants: the emergence of the social representation concept. In: Detrain C, Deneubourg J-L, Pasteels JM (eds) Information processing in social insects. Birkhäuser Verlag, Basel, pp 219–237

Lenoir A, d'Ettorre P, Errard C, Hefetz A (2001) Chemical ecology and social parasitism in ants. Annu Rev Entomol 46:573–599

Lenoir A, Depickere S, Devers S, Christides JP, Detrain C (2009) Hydrocarbons in the ant *Lasius niger*: from the cuticle to the nest and home range marking. J Chem Ecol 35:913–921

Leonhardt SD, Brandstaetter AS, Kleineidam CJ (2007) Reformation process of the neuronal template for nestmate-recognition cues in the carpenter ant *Camponotus floridanus*. J Comp Physiol 193:993–1000

Liebig J (2010) Hydrocarbon profiles indicate fertility and dominance status in ant, bee, and wasp colonies. Insect hydrocarbons: biology, biochemistry, and chemical ecology. Cambridge University Press, Cambridge, pp 254–281

Liebig J, Peeters C, Oldham NJ, Markstädter C, Hölldobler B (2000) Are variations in cuticular hydrocarbons of queens and workers a reliable signal of fertility in the ant *Harpegnathos saltator*? Proc Natl Acad Sci USA 97:4124–4131

Liu Z, Yamane S, Wang Q, Yamamoto H (1998) Nestmate recognition and temporal modulation in the patterns of cuticular hydrocarbons in natural colonies of Japanese carpenter ant *Camponotus japonicus* Mayr (Hymenoptera: Formicidae). J Ethol 16:57–65

Lockey KH (1988) Lipids of the insect cuticle: origin composition and function. Comp Biochem Physiol 89B:595–645

Lorenzi MC (1992) Epicuticular hydrocarbons of *Polistes biglumis bimaculatus* (Hymenoptera, Vespidae): preliminary results. Ethol Ecol Evol 3: 61–63, (Special Issue)

Lorenzi MC, Bagnères AG (1996) Hydrocarbon pattern variations in the paper of *Polistes biglumis bimaculatus* nests usurped or not by the social parasite *Polistes atrimandibularis* (Hymenoptera Vespidae). Proc XX Int Congr Entomol Firenze 416:13–107

Lorenzi MC, Bagnères AG, Clément JL (1996) The role of cuticular hydrocarbons in insect societies: is it the same in paper wasps? In: Turillazzi S, West Eberhard MJ (eds) Natural history and the evolution of paper wasps. Oxford University Press, Oxford, pp 178–189

Lorenzi MC, Cometto I, Marchisio G (1999) Species and colony components in the recognition odor of young social wasps: their expression and learning (*Polistes biglumis* and *P. atrimandibularis*; Hymenoptera: Vespidae). J Insect Behav 12(2):147–158

Lorenzi MC, Sledge MF, Laiolo P, Sturlini E, Turillazzi S (2004) Cuticular hydrocarbon dynamics in young adult *Polistes dominulus* (Hymenoptera: Vespidae) and the role of linear hydrocarbons in nestmate recognition systems. J Insect Physiol 50:935–941

Lorenzi MC, Caldi M, Cervo R (2007) The chemical strategies used by *Polistes nimphus* social wasp usurpers (Hymenoptera Vespidae). Biol J Linn Soc 91:505–512

Lorenzi MC, Cervo R, Bagneres A-G (2011) Facultative social parasite mark host nests with branched hydrocarbons. Anim Behav 42(5):1143–1149

Martin SJ, Vitikainen E, Helanterä H, Drijfhout FP (2008) Chemical basis of nest-mate discrimination in the ant *Formica exsecta*. Proc R Soc B 275(1640):1271–1278

Masson C, Pham-Delègue MH, Fonta C, Gascuel J, Arnold G, Nicolas G, Kerszberg M (1993) Recent advances in the concepts of adaptation to natural odour signals in the honeybee, *Apis mellifera* L. Apidologie 24:169–194

Mateo JM (2004) Recognition systems and biological organization: the perception component of recognition. Ann Zool Fennici 41:729–745

Menzel R (1993) Associative learning in honey bees. Apidologie 24:157–168

Meskali M, Bonavita-Cougourdan A, Provost E, Bagnères AG, Dusticier G, Clément JL (1995) Mechanism underlying cuticular hydrocarbon homogeneity in the ant *Camponotus vagus* (SCOP.)(Hymenoptera: Formicidae): role of postpharyngeal glands. J Chem Ecol 21(8):1127–1148

Michener CD, Smith BH (1987) Kin recognition in primitively social insects. In: Fletcher DJC, Michener CD (eds) Kin recognition in animals. John Wiley and Sons Press, Chichester, pp 209–242

Mintzer A, Vinson SB (1985) Kinship and incompatibility between colonies of the acacia-ant *Pseudomyrmex ferruginea*. Behav Ecol Sociobiol 17:75–78

Mitra A, Ramachandran A, Gadagkar R (2014) Nestmate discrimination in the social wasp *Ropalidia marginata*: chemical cues and chemosensory mechanism. Anim Behav 88:113–124

Monnin T (2006) Chemical recognition of reproductive status in social insects. Ann Zool Fenn 43:515–530

Morel L (1983) Relation entre comportement agressif et privation sociale précoce chez les jeunes fourmis immatures de la fourmi *Camponotus vagus* Scop. (Hymenoptera: Formicidae). C R Hebd Séances. Acad Sci Série D 296:449–452

Morel L (1988) Ontogènese de la reconnaissance des membres de la société chez *Camponotus floridanus* (Hymenoptera: Formicidae). Role de l'expérience sociale précoce. Biologie du Comportement 13:59–72

Newey PS, Robson SKA, Crozier RH (2009) Temporal variation in recognition cues: implications for the social life of weaver ants *Oecophylla smaragdina*. Anim Behav 77:481–488

Nielsen J, Boomsma JJ, Oldham NJ, Petersen HC, Morgan ED (1999) Colony level and season-specific variation in cuticular hydrocarbon profiles of individual workers in the ant *Formica truncorum*. Insect Soc 46:58–65

Nowbahari E, Lenoir A (1989) Age related changes in aggression in ant *Cataglyphis cursor* (Hymenoptera, Formicidae). Behav Process 18:173–181

Ozaki M, Hefetz A (2014) Neural mechanisms and information processing in recognition systems. Insects 5:722–741

Ozaki M, Wada-Katsumata A (2010) Perception and olfaction of cuticular compounds. In: Blomquist GJ, Bagnères AG (eds) Insect hydrocarbons: biology, biochemistry and chemical ecology. Cambridge University Press, Cambridge, pp 207–221

Ozaki M, Wada-Katsumata A, Fujikawa K, Iwasaki M, Yokohari F, Satoji Y, Nisimura T, Yamaoka R (2005) Ant nestmate and non-nestmate discrimination by a chemosensory sensillum. Science 309:311–314

Page RE, Breed ME (1987) Kin recognition in social bees. Trends Ecol Evol 2:272–275

Panek LM, Gamboa GJ, Espelie KE (2001) The effect of a wasp's age on its cuticular hydrocarbon profile and its tolerance by nestmate and non-nestmate conspecifics (*Polistes fuscatus*, Hymenoptera: Vespidae). Ethology 107:55–63

Pauls D, Selcho M, Gendre N, Stocker RF, Thum AS (2010) *Drosophila* larvae establish appetitive olfactory memories via mushroom body neurons of embryonic origin. J Neurosci 30:10655–10666

Peeters C, Monnin T, Malosse C (1999) Cuticular hydrocarbons correlated with reproductive status in a queenless ant. Proc R Soc Lond B 266:1323–1327

Pfenning DW, Reeve HK, Shellmann JS (1983a) Learned component of nestmate discrimination in workers of a social wasp, *Polistes fuscatus* (Hymenoptera, Vespidae). Anim Behav 31:412–416

Pfenning DW, Gamboa GJ, Reeve HK, Shellmann JS, Reeve JS, Ferguson ID (1983b) The mechanism of nestmate discrimination in social wasps (Hymenoptera: Vespidae). Behav Ecol Sociobiol 13:299–305

Provost E, Blight O, Tirard A, Renucci M (2008) Hydrocarbons and insects' social physiology. In: Maes RP (ed) Insect physiology: new research. Nova Science Publishers, New York, pp 19–72

Python F, Stocker RF (2002) Adult-like complexity of the larval antennal lobe of *D. melanogaster* despite markedly low numbers of odorant receptor neurons. J Comp Neurol 445:374–387

Ramaekers A, Magnenat E, Marin EC, Gendre N, Jefferis GSXE, Luo L, Stocker RF (2005) Glomerular maps without cellular redundancy at successive levels of the *Drosophila* larval olfactory circuit. Curr Biol 15:982–992

Ratnieks FL (1991) The evolution of genetic odor-cue diversity in social Hymenoptera. Am Nat pp 202–226

Ray S (1999) Survival of olfactory memory through metamorphosis in the fly *Musca domestica*. Neurosci Lett 259:37–40

Reeve HK (1989) The evolution of conspecific acceptance thresholds. Am Nat 133:407–435

Robinson SR, Smotherman WP (1991) Fetal learning: implications for the development of kin recognition. In: Hepper PG (ed) kin recognition. Cambridge University Press, Cambridge, England, pp 308–334

Ross NM, Gamboa GJ (1981) Nestmate discrimination in social wasps (*Polistes metricus*, Hymenoptera: Vespidae). Behav Ecol Sociobiol 9:163–165

Schaal B, Marlier L, Soussignan R (2000) Human fetuses learn odours from their pregnant mother's diet. Chem Sens 25:729–737

Shellman JS, Gamboa GJ (1982) Nestmate discrimination in social wasps: the role of exposure to nest and nestmates. Behav Ecol Sociobiol 11:51–53

Signorotti L, Cappa F, d'Ettorre P, Cervo R (2014a) Novel insights into the ontogeny of nestmate recognition in *Polistes* social wasps. PLoS ONE 9(5):e97024

Signorotti L, Jaisson P, d'Ettorre P (2014b) Larval memory affects adult nestmate recognition in the ant *Aphaenogaster senilis*. Proc R Soc B 281:20132579

Singer TL (1998) Roles of hydrocarbons in the recognition systems of insects. Am Zool 38(2):394–405

Singer TL, Espelie KE (1992) Social wasps use nest paper hydrocarbons for nestmate recognition. Anim Behav 44(1):63–68

Singer TL, Camann MA, Espelie KE (1992) Discriminant analysis of cuticular hydrocarbons of social wasp *Polistes exclamans* Viereck and surface hydrocarbons of its nest paper and pedicel. J Chem Ecol 18:785–797

Singh RN, Singh K (1984) Fine structure of the sensory organs of *Drosophila melanogaster* Meigen larva (Diptera: Drosophilidae). Int J Insect Morphol Embryol 13:255–273

Sledge MF, Trinca I, Massolo A, Boscaro F, Turillazzi S (2004) Variation in cuticular hydrocarbon signatures, hormonal correlates and establishment of reproductive dominance in a polistine wasp. J Insect Physiol 50:73–83

Soroker V, Vienne C, Hefetz A, Nowbahari E (1994) The postpharyngeal gland as a “gestalt” organ for nestmate recognition in the ant *Cataglyphis niger*. Naturwissenschaften 81:510–513

Soroker V, Vienne C, Hefetz A (1995) Hydrocarbon dynamics within and between nestmates in *Cataglyphis niger* (Hymenoptera: Formicidae). J Chem Ecol 21(3):365–378

Soroker V, Fresneau D, Hefetz A (1998) Formation of colony odor in ponerine ant *Pachycondyla apicalis*. J Chem Ecol 24(6):1077–1090

Soroker V, Lucas C, Simon T, Fresneau D, Durand JL, Hefetz A (2003) Hydrocarbon distribution and colony odour homogenization in *Pachycondyla Apicalis*. Insect Soc 50:212–217

Starks PT (2004) Recognition systems: from components to conservation. In: Annales Zoologici Fennici, vol 41(6). Suomen Biologian Seura Vanamo, Helsinki, pp 689–690 (1964-)

Stroeymeyt N, Guerrieri FJ, van Zweden JS, d’Ettorre P (2010) Rapid decision-making with side-specific perceptual discrimination in ants. PLoS ONE 5(8):e12377

Stuart RJ (1987a) Nestmate recognition in leptothoracine ants: testing Fielde’s progressive odor hypothesis. Ethology 76(2):116–123

Stuart RJ (1987b) Individual workers produce colony-specific nestmate recognition cues in the ant, *Leptothorax curvispinosus*. Anim Behav 35:1062–1069

Stuart RJ (1988) Collective cues as a basis for nestmate recognition in polygynous leptothoracine ants. Proc R Soc B 85(12):4572–4575

Stuart RJ (1992) Nestmate recognition and the ontogeny of acceptability in the ant, *Leptothorax curvispinosus*. Behav Ecol Sociobiol 30:403–408

Sturgis S, Gordon DM (2012) Nestmate recognition in ants (Hymenoptera, Formicidae): a review. Myrmecological News 16:101–110

Tibbetts EA (2002) Visual signals of individual identity in the wasp *Polistes fuscatus*. Proc R Soc B 269(1469):1423–1428

Tissot M, Stocker RF (2000) Metamorphosis in *Drosophila* and other insects: the fate of neurons throughout the stages. Prog Neurobiol 62(1):89–111

Turillazzi S (1985) Function and characteristics of the abdominal substance secreted by wasps of the genus *Parischnogaster* (Hymenoptera Stenogastrinae). Monit Zool Ital 19:91–99

Turillazzi S, Cervo R, Cavallari I (1990) Invasion of the nest of *Polistes dominulus* by the social parasite *Sulcopolistes sulcifer* (Hymenoptera, Vespidae). Ethology 84:47–59

Turillazzi S, Sledge MF, Dani FR, Cervo R, Massolo A, Fondelli L (2000) Social hackers: integration in the host chemical recognition system by a paper wasp social parasite. Naturwissenschaften 87(4):172–176

Turillazzi S, Fanelli D, Theodora P, Lambardi D, Ortolani I, Hashim R, Baracchi D (2008) Determinants of immature brood and nest recognition in a stenogastrine wasp (Hymenoptera Vespidae). Ethol Ecol Evol 20(1):17–33

Tully T, Cambiazo V, Kruse L (1994) Memory through metamorphosis in normal and mutant *Drosophila*. J Neurosci 14:68–74

Vander Meer RK, Morel L (1998) Nestmate recognition in ants. In: Vander Meer RK, Breed MD, Winston M, Espelie C (eds) Pheromone communication in social insects: ants, wasps, bees and termites, pp 79–103

Van Hooser CA, Gamboa GJ, Fishwild TG (2002) The function of abdominal stroking in the paper wasp, *Polistes fuscatus* (Hymenoptera Vespidae). Ethol Ecol Evol 14(2):141–148

Van Oystaeyen A, Oliveira RC, Holman L, van Zweden JS, Romero C, Oi CA, d'Ettorre P, Khalesi M, Billen J, Wäckers F, Millar JG, Wenseleers T (2014) Conserved class of queen pheromones stops social insect workers from reproducing. Science 343(6168):287–290

van Zweden JS, d'Ettorre P (2010) Nestmate recognition in social insects and the role of hydrocarbons. In: Blomquist GJ, Bagnères AG (eds) Insect hydrocarbons: biology, biochemistry and chemical ecology. Cambridge University Press, Cambridge, pp 222–243

van Zweden JS, Dreier S, d'Ettorre P (2009) Disentangling environmental and heritable nestmate recognition cues in a carpenter ant. J Insect Physiol 55:158–163

van Zweden JS, Brask JB, Christensen JH, Boomsma JJ, Linksvayer TA, d'Ettorre P (2010) Blending of heritable recognition cues among ant nestmates creates distinct colony gestalt odours but prevents within-colony nepotism. J Evol Biol 23(7):1498–1508

Vienne C, Bagnères AG, Lange C, Errard C (1990) Etude chimique de la reconnaissance interindividuelle chez *Myrmica rubra* et *Manica rubida* (Formicidae, Myrmicinae) élevées en colonies mixtes artificielles. Actes Colloq Insectes Soc 6:261–265

Vienne NC, Soroker V, Hefetz A (1995) Congruency of hydrocarbon patterns in heterospecific groups of ants: transfer and/or biosynthesis? Insect Soc 42(3):267–277

Wagner D, Brown MJF, Broun P, Cuevas W, Moses LE, Chao DL, Gordon DM (1998) Task related differences in the cuticular hydrocarbon composition of harvester ants, *Pogonomyrmex barbatus*. J Chem Ecol 24:2021–2037

Waldman B (1988) The ecology of kin recognition. Ann Rev Ecol Syst 19:543–571

Wilson EO (1971) The insect societies. Belknap Press of Harvard University Press, Cambridge

Zacchi F, Cervo R, Turillazzi S (1996) How *Polistes semenowi*, obligate social parasite, invades the nest of its host, *Polistes dominulus* (Hymenoptera, Vespidae). Insect Soc Life 1:125–130

Zahavi A (1977) Reliability in communication system and the evolution of altruism. In: Stonehous B, Perrins C (eds) Evolutionary ecology. University Park Press, Baltimore