



# Nestmate Recognition in Social Insects: What Does It Mean to Be Chemically Insignificant?

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Social insects use the blend of hydrocarbons present on their cuticle to efficiently distinguish nestmates from aliens. Intruders must therefore find a strategy to break the recognition code in order to exploit the colony resources. Twenty years ago, the concept of “chemical insignificance” was introduced to characterize those parasites bearing almost no recognition cues on their cuticle, thus appearing chemically undetectable to their hosts. In some cases, intruders do possess cuticular hydrocarbons, but these are present in lower amount with respect to their hosts and/or they belong to different classes than the hydrocarbons typically used as recognition cues. We propose to include these cases under the label of chemical insignificance. If chemical compounds are absent on the cuticle of the intruder, or if they are produced but not perceived by the host (e.g., below the detection threshold), or if they are perceived but not meaningful, in all cases the result is identical: the profile of the intruder appears chemically neutral; thus, it is irrelevant for the host. We also discuss the consequences of producing low amounts of cuticular hydrocarbons, given that their original function is to act as a barrier against desiccation. Clarifying the concept of chemical insignificance will help unify terminology and stimulate interdisciplinary research efforts involving simultaneous investigations of chemical profiles, behavior, and physiology to elucidate the proximate and ultimate mechanisms characterizing the co-evolutionary arms race between hosts and parasites.

**Keywords:** ants, bees, wasps, cuticular hydrocarbons, social parasites

Twenty years after the concept of “chemical insignificance,” characterizing insect parasites bearing almost no recognition cues on their cuticle, was introduced (Lenoir et al., 1999, 2001), several comparable chemical adaptations have been described in the literature, often using different terminology. In this perspective, we briefly review the use of these different terms and propose to include all of them under the label “chemical insignificance.” Using multiple terms to address a phenomenon that appears to have similar adaptive significance in different species can hinder the comprehension of both its underlying proximate mechanisms and evolutionary pathway.

## CUTICULAR HYDROCARBONS AS RECOGNITION CUES

Social insects use the complex blend of hydrocarbons present on their cuticle for nestmate recognition (Lenoir et al., 1999; Dani, 2006; Blomquist and Bagnères, 2010; d'Ettorre and Lenoir, 2010). This mixture is composed of different classes of hydrocarbons, such as linear alkanes, methyl-branched alkanes, and alkenes, with a chain length typically ranging from 20 to 40

carbon atoms, although in some cases, heavier hydrocarbons have been detected. The cuticular hydrocarbon (CHC) profile is species-specific, meaning that different species show qualitatively different CHC mixtures, characterized by a species-specific combination of compounds (Bagnères and Wicker-Thomas, 2010). The CHC profile is also colony-specific, implying that within a given colony, the “colony odor” is generally uniform, but different colonies of the same species show quantitatively different profiles, i.e., different relative proportions of the same hydrocarbons. The homogeneity of the colony odor is maintained by exchanges via trophallaxis, allogrooming, and/or contact with the nest material (Lenoir et al., 1999).

## DEFICIENCY OF RECOGNITION CUES IN CALLOWS AND PARASITES

Remarkably, some individuals do not show the typical species/colony CHC profile. Newly enclosed (callow) social insect workers usually possess very low amounts of CHCs at emergence and can be experimentally transferred from one colony to another, even a different species, without eliciting an aggressive response from adult workers (e.g., ants: Errard, 1994; wasps: Lorenzi et al., 1999; bees: Breed et al., 2004). Lenoir et al. (1999) termed this lack of chemical recognition cues “chemical insignificance.” Young workers then go through a process of chemical integration by synthesizing CHCs and also by acquiring them via interactions with colony members (allogrooming, trophallaxis) and contacts with nest material (Bos et al., 2011). This ontogeny of the CHC profile can last several days; for instance, workers of the ant *Aphaenogaster senilis* acquire a CHC profile typical of adults in about 20 days (Ichinose and Lenoir, 2009), while it takes about 4 days in *Bombus terrestris* (Sramkova and Ayasse, 2009). *Polistes* wasps acquire the adult CHC profile in about 3 days, during which they increase drastically the total amount of the hydrocarbons but also incur a qualitative change: the proportion of branched hydrocarbons increases at the expense of that of linear hydrocarbons and relatively long-chain hydrocarbons increase at the expense of short-chain ones (Lorenzi et al., 2004a).

The concept of chemical insignificance has been extended to social parasites (Lenoir et al., 1999, 2001) that need to infiltrate and be tolerated into a host nest. Lacking conspicuous recognition cues may help both remaining undetected when entering a host colony and facilitating the acquisition of the colony odor from the nest material and the hosts. Chemical insignificance works effectively if the host recognition system is based on the undesirable-present (U-present) model, and not on a point-by-point label/template matching. In the U-present model, rejection by the discriminator is elicited only by the presence of additional/odd cues on the intruder, either different compounds or higher amounts of some compounds that are also present of the cuticle of the discriminator (Guerrieri et al., 2009; van Zweden and d’Ettorre, 2010). The underlying perceptual mechanism may act at the level of the antennae (Ozaki et al., 2005; Ozaki and Hefetz, 2014) or at higher levels (e.g., antennal lobes: Guerrieri et al., 2009; Brandstaetter et al.,

2011), although these two models are not mutually exclusive (Bos and d’Ettorre, 2012). Therefore, when the incoming individual bears no detectable cues, theory predicts that the individual will not be rejected. A reduced amount of recognition cues on the cuticle (with respect to residents) has the same effect as the absence of cues, providing that the amount does not reach the detection threshold of the discriminator. Data on the detection threshold of social insects are very scarce. We know that ants can detect very low amounts of hydrocarbons, namely, a total CHC extract equivalent of  $10^{-4}$  workers in *A. senilis* (Ichinose and Lenoir, 2010), and can discriminate different concentrations of the same hydrocarbon, with one concentration as low as 0.3 ant equivalents (*Camponotus aethiops*, Di Mauro et al., 2015). Foundresses of the paper wasp *Polistes dominula* start reacting aggressively when presented with lures carrying the two-thirds of the total surface extract obtained from one wasp, while the reaction to one-third of the extract does not differ from the reaction to the solvent alone (Cini et al., 2009), suggesting that paper wasps might have a higher detection threshold than ants.

## CHEMICAL INSIGNIFICANCE AND CHEMICAL TRANSPARENCY

Not all the classes of hydrocarbons are good candidates to act as recognition cues. There is evidence that methyl-branched alkanes and alkenes are more important than linear alkanes in the recognition process (review in van Zweden and d’Ettorre, 2010). Consequently, a cuticular profile characterized by linear alkanes and a reduced number/amount of the other hydrocarbon classes may also be chemically undetectable in the context of nestmate recognition. The production of a profile characterized by the presence of hydrocarbons that are not used as recognition cues has been termed “chemical transparency” (Martin et al., 2008). For example, adults and eggs of the social parasite *Vespa dybowskii* show a chemical profile dominated by alkanes and alkenes, while methyl-branched compounds are only present in traces (<1%). These methylated compounds, which act as recognition cues in hornets, are instead present in high proportion in the host species *V. simillima* (41%) (Martin et al., 2008). Larvae of the paper wasp social parasite *Polistes sulcifer* appear to use a similar strategy, as their cuticular profile shows a higher relative proportion of linear alkanes but a lower proportion of branched and unsaturated hydrocarbons than the profile of host larvae, *P. dominula* (Cervo et al., 2008). Similarly, the parasite *Polistes atrimandibularis* larvae show higher proportion of linear alkanes compared to their host larvae (Elia et al., 2018). In these examples, even if the total amount of CHCs is similar in hosts and parasites, the relative amount of key compounds is significantly lower in parasites (see also **Table 1**). Therefore, these parasites produce a chemical mixture that is “invisible” to the host in the recognition context and therefore does not elicit aggression. We propose that these cases of so-called chemical transparency or chemical neutrality should be included under the broader label of chemical insignificance. Moreover, chemical insignificance, in the form of reduced total amount of CHCs, might compensate for potentially “visible”

traits in the parasite CHC profile, for instance, the presence of relatively short-chain CHCs (which are in principle conspicuous) in *P. atrimandibularis* parasites before they invade a host nest (Uboni et al., 2012), or the “imperfect” mimicry of the cuckoo wasp, *Hedychrum rutilans* (Kroiss et al., 2009) (Table 1).

Another aspect to be considered is the hydrocarbon chain length. Very-long-chain hydrocarbons are characterized by low volatility and thus are relatively more difficult to perceive for the discriminator by olfaction, which is the usual way of hydrocarbon detection (Brandstaetter et al., 2008). Producing a CHC profile shifted toward long-chain hydrocarbons could be a form of chemical insignificance (Lambardi et al., 2007). However, this does not seem to be the general case, at least for the examples listed in Table 1, in which—if anything—we observe sometimes the opposite trend, with parasites having a profile characterized by lighter compounds than their hosts. An intriguing case is that of parabolic ant species, in which a large-scale comparison highlighted that associated species show significantly longer CHCs and higher proportions of methyl-branched alkenes (very rare compounds among insects) and alkadienes than non-associated species, suggesting that the evolution of interspecific amicable associations is linked to a shift toward higher chain lengths (Menzel and Schmitt, 2012).

## WHY PRODUCE HYDROCARBONS?

If the lack of CHCs facilitates integration into the host colony, one should expect the totality of parasites being denuded of these cues. Yet, we observe the majority of them producing at least a minimum amount (e.g., 20% of the amount found in the hosts, Kroiss et al., 2009; Uboni et al., 2012). The original function of hydrocarbons is protection against desiccation and also pathogens and toxins; hence, parasites might be obliged to produce them. However, not all hydrocarbon classes are suitable to prevent desiccation. Linear alkanes (n-C20-C40), especially with long chain, are better than other classes in limiting dehydration as they are solid and in a relatively impermeable state at temperatures <40°C, while they begin melting and become more water permeable at higher temperatures (Gibbs and Pomonis, 1995). When alkanes are blended with unsaturated CHC (alkenes) or methylated (branched) alkanes, the resulting blend is characterized by a lower melting temperature than a blend composed exclusively of linear alkanes, and thus it becomes more permeable and less effective as a waterproofing barrier (Gibbs and Rajpurohit, 2010). The cuticular layer of social parasites is typically relatively rich in linear alkanes with respect to their hosts (Table 1), which may increase cuticle impermeability and counterbalance the overall low amount of CHCs. However, the relationships between CHC composition and their physical properties may be more complex: the physical properties of complex blends, such as those that characterize the cuticular layer of insects, are poorly understood and their waterproofing properties are rarely studied (Gibbs and Rajpurohit, 2010). Even the presumptive correlation between amount of hydrocarbons and waterproofing (Hadley, 1981) does not always hold. For instance, several species of *Cataglyphis*

desert ants, which forage at high temperature, have considerably lower total amount of CHCs (about ¼) than *Myrmica* ants, which live in humid boreal forests, but *Cataglyphis* ants lose less water than *Myrmica* ants due to a lower transpiration rate (Lenoir et al., 2009). The profile of *Cataglyphis* is characterized by a higher proportion of saturated compounds and a lower proportion of alkenes compared to that of *Myrmica*. Therefore, physiological adaptations may contribute to water balance and counteract effectively a low amount of CHCs, as well as morphological adaptations, such as a thicker cuticle in parasites compared to their hosts (Cervo, 1994). In addition, chemically insignificant parasites might compensate for the costs of a higher potential for desiccation through specific behavioral strategies. For instance, they might spend more time than their hosts in less dry, shadowy, parts of the nest, or increase the ingestion of liquids, e.g., by soliciting trophallaxis from the hosts. Preliminary field data on the parasitic wasp *P. atrimandibularis* are consistent with this hypothesis: parasites appear to avoid direct sunlight by seeking the shade (they are less active than the hosts and rest more time behind the nest in the part not exposed to the sun), and they are more involved than their hosts in trophallactic exchanges as recipients, rather than as donors (Lorenzi, personal observation).

## DISCUSSION

We show that there are at least three different ways in which parasitic insects can wear a cloak of chemical invisibility in order to facilitate the intrusion and tolerance in a host nest: (i) the total absence of CHCs, (ii) the production of a reduced amount of CHCs (below the discriminator's detection threshold), and (iii) the production of hydrocarbons that are not used as recognition cues.

In the first case, CHCs are virtually totally lacking from the cuticle of the intruder, thus preventing hosts from detecting any chemical cue that might inform them about the presence of the intruder. While this was the original observation that prompted the emergence of the term chemical insignificance (Lenoir et al., 1999, 2001) in some social parasites of ants, subsequent discoveries in other insects have offered less drastic examples of paucity of recognition cues (reviewed in Bagnères and Lorenzi, 2010). Bearing a reduced amount of CHCs with respect to the host target, the second case that we highlight is a relatively more common adaptation and may result in intruders sneaking into host nests undetected, or at least not detected enough to elicit the most violent rejection. If the amount of cues falls below or around the detection threshold of the host, the amount of aggression will be limited, as suggested by the observation that the level of aggressive responses is positively correlated to the total amount of recognition cues on lures in wasps and ants (Cini et al., 2009; Ichinose and Lenoir, 2010).

Finally, the chemical profile of intruders may be composed of hydrocarbons that are not primarily important in the nestmate recognition process. For instance, bearing a higher proportion of linear alkanes, rather than branched alkanes, is a common characteristic among social parasites. If only part of the chemical

**TABLE 1** | Characteristics of the CHC profile of parasites that differ from that of hosts (calculated as “parasites minus hosts”).

Parasite (type)	Host	Reduced CHC total amount	Proportion of CHC by class	Difference in chain-length	Reference
<i>Polistes atrimandibularis</i> (social parasite)	<i>P. biglumis</i>	Yes	>LA >E <BA	Lighter	Lorenzi and Bagnères, 2002; Uboni et al., 2012
<i>Polistes semenowi</i> (social parasite)	<i>P. dominula</i>	Yes	No	Lighter	Lorenzi et al., 2004b; Lorenzi, personal observation
<i>Polistes sulcifer</i> (social parasite)	<i>P. dominula</i>	Yes	>LA <BA	Possibly lighter	Turillazzi et al., 2000; Sledge et al., 2001
<i>Bombus sylvestris</i> (social parasite)	<i>B. pratorum</i>	Yes			Dronnet et al., 2005
<i>Polyergus rufescens</i> (social parasite)	<i>Formica cunicularia</i>	Yes	Almost no CHC		Lenoir et al., 2001
<i>Polyergus breviceps</i> (social parasite)	<i>Formica gnava</i>	Yes	Almost exclusively LA		Johnson et al., 2001
<i>Polyergus samurai</i> (social parasite)	<i>F. japonica</i>	Yes	Almost exclusively LA		Tsuneoka and Akino, 2012
<i>Acromyrmex insinuator</i> (social parasite)	<i>A. echinator</i>	Yes	>LA	Contradictory results: Heavier than host Lighter than host	Lambardi et al., 2007; Nehring et al., 2015
<i>Temnothorax</i> sp. (social parasite)	<i>Temnothorax</i> sp.	No	>LA <BA	Lighter	Kleeberg et al., 2017
<i>Formicoxenus provancheri</i> (xenobiont)	<i>Myrmica incompleta</i>	Yes		Acquired mimicry	Lenoir et al., 1997, 2001
<i>Ectatomma ruidum</i> (cleptobiont)	<i>Ectatomma ruidum</i>	Yes	Same species, no qualitative differences		Jeral et al., 1997
<i>Attaphila</i> sp. (myrmecophilous cockroach)	<i>Acromyrmex octospinosus</i> , <i>Atta colombica</i>	Yes, <i>Acromyrmex</i> No, <i>Atta</i>	No	No	Nehring et al., 2016
<i>Mutilla europaea</i> (cleptobiont)	<i>Polistes biglumis</i>	Yes	>LA >E <BA	Lighter	Uboni et al., 2012
<i>Hedychrum rutilans</i> (parasitoid)	<i>Philanthus triangulum</i>	Yes, but also mimicry	No	No	Kroiss et al., 2009
<i>Sternocoelis hispanus</i> (myrmecophilous beetle)	<i>Aphaenogaster senilis</i>	No		Mimicry	Lenoir et al., 2012
Silverfish (myrmecophilous)	<i>Aphaenogaster senilis</i>	Yes	>LA <BA	Lighter	Lenoir et al., 2012

“Parasite” is used as a general term, including parasitoids, cleptobionts, and myrmecophilous species. For social parasites, we refer to the phase before host nest invasion; for hosts, we refer either to the same phase, or to unparasitized hosts.

“>”: larger in parasites than in hosts; “<”: smaller in parasites.

LA, linear alkanes; BA, branched alkanes; E, alkenes. Cells are empty when the information is not available.

profile informs about the identity of the bearer, lacking that part is equivalent to being chemically insignificant.

It could be argued that alternative explanations exist for the observed large difference in the total amount of CHCs between social parasites and hosts. For instance, hosts may not necessarily express a minimum amount of CHCs to avoid dehydration, they could have an excessive amount of CHCs on their cuticle to serve recognition purposes (the “host chemical over-significance” hypothesis). In this view, the amount of CHCs on the social parasite cuticle, despite being lower than that of the host, might be enough to prevent dehydration. In our opinion, this hypothesis is less parsimonious than that of chemical insignificance, since CHCs are supposed to be costly to produce and therefore hosts might incur high costs for overexpressing

them (e.g., d'Ettorre and Heinze, 2001; Holman et al., 2010). Moreover, the chemical over-significance hypothesis calls for different explanations even among closely related species of social parasites. Young queen of *Polyergus rufescens* social parasites have virtually no CHCs, while *Polyergus breviceps* and *P. samurai* have some but less CHCs than their hosts. Under the chemical insignificance hypothesis, the three *Polyergus* species employ the same strategy, and differ only in the how extreme their strategy is; under the chemical over-significance hypothesis, the lack of CHC in *P. rufescens* is not easily explained. Finally, there is evidence for a gradual mode of evolution of CHCs in ants (van Wilgenburg et al., 2011), which also contradicts this alternative hypothesis.

A total lack of recognition cues, a diluted chemical profile, or the lack of hydrocarbons relevant in recognition processes

may be parsimoniously interpreted as parasite adaptation that serve the same function: sneaking into host nests undetected. In a review about terminology, von Beeren et al. (2012) suggest the term “chemical hiding” when an organism shows the total absence of recognition cues or the presence of cues below the discriminator detection threshold (thus not detectable), as opposed, for instance, to “chemical masquerade” (detected but misidentified as uninteresting entity, eliciting no reaction) and “chemical mimicry” (resembling an interesting entity, such as a nestmate). However, one can hide by resembling something else; therefore, we believe that a functional approach might be more practical than focusing on terms. Furthermore, “chemical insignificance” is now a term widely employed in the social insect literature, and it might be more difficult to replace it than to clarify its meaning by including the three functional categories presented here.

The different ways of being chemically insignificant are not mutually exclusive: for instance, invading females of the social parasite *P. atrimandibularis*, as well as females of the cleptoparasite *Mutilla europaea*, are chemical insignificant by producing only 20% of the total amount of CHCs compared to their host, and also express primarily linear alkanes, at the expense of the more informative branched alkane component of the profile (Uboni et al., 2012). Chemical insignificance offers a protection against detection, but it might also be a way to facilitate the acquisition of host colony odor (Lenoir et al., 2001; Lorenzi et al., 2004b; Lorenzi, 2006). This hypothesis stems from the observation that newly eclosed social insects are typically chemical insignificant (i.e., poor in recognition cues) and acquire the colony odor with time (Lenoir et al., 1999). Chemical insignificance may be not completely effective: *Polyergus* queens, as well as *P. atrimandibularis* parasites or *Hedychrum*, are regularly attacked when they infiltrate the host colony, which means that other cues elicit the reaction of the hosts. For instance, visual cues might be used by residents (e.g., visual cues have a role in interactions among nestmates in wasps) as well as tactile cues, which might help distinguish a chemically insignificant parasite from the background.

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Finally, what is especially surprising is that, at least in social insects, chemical insignificant social parasites share the same habitat as their hosts: they live in the same colony and are exposed to the same physical stressors (e.g., solar radiation, heat, dryness) as their hosts, and therefore are likely to share similar physiological requirements to cope for water loss (Lorenzi, 2006). If CHCs act as a protective barrier, chemical insignificant parasites have to find a solution to reduce the impact of these stressors. One testable hypothesis is that behavioral modifications (e.g., minimizing direct exposure to sunlight, reducing general activity, and increasing introduction of liquids) may compensate for the deficiency of CHCs.

The data are currently too scanty to draw conclusions, yet preliminary measures of total CHC quantities and environmental parameters suggest that the association between the amount of CHCs and dehydration risk may be mediated by modifications involving other traits, such as behavior and physiology. We hope that clarifying the concept of chemical insignificance by using a functional approach will help both unify terminology and broaden interdisciplinary research effort involving simultaneous investigations on chemical ecology, behavioral adaptations, and water balance physiology.

## AUTHOR CONTRIBUTIONS

ML and PE conceived and wrote the paper.

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**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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