Biochemical Systematics and Ecology 51 (2013) 335–342

Contents lists available at ScienceDirect

Biochemical Systematics and Ecology

journal homepage: www.elsevier.com/locate/biochemsyseco

Chemical integration of *Thorictus* myrmecophilous beetles into *Cataglyphis* ant nests

Alain Lenoir [a,*], Jiří Háva [b,c], Abraham Hefetz [d], Abdallah Dahbi [e], Xim Cerdá [f], Raphaël Boulay [a]

[a] *IRBI, Institut de Recherche sur la Biologie de l'Insecte, UMR CNRS 6035, Université François Rabelais de Tours, Faculté des Sciences, Parc de Grandmont, 37200 Tours, France*
[b] *Department of Forest Protection and Entomology, Faculty of Forestry and Wood Sciences, Czech University of Life Sciences, Kamýcká 1176, CZ-165 21 Prague 6, Suchdol, Czech Republic*
[c] *Private Entomological Laboratory & Collection, Rýznerova 37/37, CZ-252 62 Únětice u Prahy, Prague-West, Czech Republic*
[d] *Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv 69978, Israel*
[e] *Equipe ENSA (Environnement et Santé), Département des Sciences Naturelles, Université Cadi Ayyad, Faculté Polydisciplinaire, Safi, Morocco*
[f] *Estación Biológica de Doñana (CSIC), Av. Américo Vespucio, 41092 Sevilla, Spain*

ARTICLE INFO

Article history:
Received 9 July 2013
Accepted 5 October 2013
Available online

Keywords:
Cataglyphis
Ants
Hydrocarbons
Thorictus
Chemical mimicry
Myrmecophilous beetles

ABSTRACT

Thorictus beetles of the Dermestidae are obligate myrmecophiles. To understand how these beetles are integrated into and tolerated by their host colonies, the cuticular hydrocarbon profiles of different species of the *Thorictus castaneus* group that are generally associated with *Cataglyphis* were examined. The beetles are characterized by small amounts of cuticular hydrocarbons, which render them partly chemically "insignificant". They also have the same cuticular hydrocarbon profiles as their hosts and thus likely use chemical mimicry to evade worker hostility but, like slaves in slave-maker species, they maintain some partial chemical identity. *Thorictus martinezi* from Burkina Faso were immediately adopted by conspecific colonies of their host, *Cataglyphis* sp. aff. *bicolor*, but were never adopted by colonies of other species (i.e. *Cataglyphis viatica* and *Formica selysi*). *Thorictus buigasi* from Morocco also mimicked the chemical profile of its host, *C. viatica*, but, in contrast to *T. martinezi*, individuals were adopted by colonies of *Cataglyphis velox* from Spain. This result can be explained by the similarity between the hydrocarbon profiles of *C. viatica* and *C. velox*, which may facilitate adoptions. *T. buigasi* beetles remained in *Formica selysi* colonies for some time but were ultimately rejected, probably due to their very different hydrocarbon profiles. In contrast, they were sometimes adopted by *Camponotus herculeanus* colonies and eventually chemically matched their new hosts, probably by passive camouflage. These data suggest that *Thorictus* of *castaneus* group myrmecophily is the result of coevolution with *Cataglyphis* hosts and that the mimicry is plastic, such that beetles can live with different hosts if the hosts show very limited CHC differences.

1. Introduction

Social insect nests, such as those of ants and termites, offer favorable environments and food resources that host microcosms of other organisms, mostly arthropods (Wilson, 1971; Hölldobler and Wilson, 1990; Schmid-Hempel, 1998;

* Corresponding author. Tel.: +33 247367333.
E-mail address: alain.lenoir@univ-tours.fr (A. Lenoir).

0305-1978/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.bse.2013.10.002

Kronauer and Pierce, 2011; Cristaldo et al., 2012). Interactions between ants and mymecophiles can be predatory, commensal (consumption of ant food remains), mutualistic, or parasitic in nature. However, in order to be accepted in an ant nest, mymecophiles must confront the chemical recognition system that ant workers use to recognize and exclude aliens. More specifically, a colony-specific mixture of cuticular hydrocarbons (CHCs) has been shown to constitute the recognition pheromone of most ant species (Hefetz, 2007; D'ettorre and Lenoir, 2010).

Several myrmecophile integration strategies have previously been described, and varying strategies can even coexist in the same host-species system (Stoeffler et al., 2011). Some myrmecophiles, such as the three *Pella* species that live in *Lasius fuliginosus* colonies, do not utilize chemical mimicry but instead evade host hostility by simply escaping from aggressive ants or using appeasement or repelling behaviors (Stoeffler et al., 2011). Myrmecophiles can also chemically mimic their hosts either by biosynthesizing host hydrocarbons *de novo* or by actively or passively acquiring them from their host. Chemical mimicry employing *de novo* biosynthesis of the host's hydrocarbons is relatively rare. It was shown to occur more than 30 years ago in four species of the termitophilous genus *Trichopsenius*, which contains species that are real mimics of their *Reticulitermes* hosts (Howard et al., 1980, 1982), and more recently in *Sternocoelis* beetles that are guests of *Aphaenogaster senilis* (Lenoir et al., 2012). Myrmecophilous aphids may also actively produce hydrocarbons that resemble those of the tending ant *Lasius fuji* (Endo and Itino, 2013). However, hydrocarbons are more commonly acquired from respective hosts through cuticular contacts and/or grooming, e.g., by actively licking the host's cuticle; this strategy is also called chemical camouflage (see reviews by (Lenoir et al., 2001; Akino, 2008; Bagnères and Lorenzi, 2010; Von Beeren et al., 2011). Myrmecophiles, such as woodlice, mites, phorid flies, and snails, can also be chemically "insignificant": their cuticles bear only small amounts of hydrocarbons, as has been shown in inquilines of *Leptogenys distinguenda* colonies (Witte et al., 2008). Similarly, callow ants are chemically insignificant, which allows them to be accepted in alien colonies during the first hours after emergence (see (Lenoir et al., 1999)). Another integration mechanism has recently been discovered in social insects: parasites can be chemically "transparent" if they bear only saturated hydrocarbons, but the relevance of this strategy for myrmecophiles is not yet known (Martin et al., 2008).

All species in the genus *Thorictus* are myrmecophilous and demonstrate two types of life history patterns with regards to their hosts. Some are *Cataglyphis* specialists, such as *Thorictus foreli*, a system that was described early on by authors like Wasmann and Forel (see Wheeler (1910) and again later by other researchers (Reichensperger, 1925; Banck, 1927). These *Thorictus* species are phoretic, i.e., they remain attached to ant antennae. Phoresy is the name of the association in which an organism attaches itself to a host body part and is subsequently transported by its host (see Kistner (1979) for examples in insects). Others, like *Thorictus grandicollis*, roam freely in the nest and are hosted by various ant species (*Messor*, *Pheidole*, etc.); they are considered to be generalists (Cammaerts and Cammaerts, 1994). All the *Thorictus* species, specialists and generalists, are deemed to be mainly detritivorous (Sanchez-Pinero and Gomez, 1995).

Here, data are presented on the chemical integration of various myrmecophilous *Thorictus* beetles found in association with various *Cataglyphis* species. To investigate host specificity, attempts were made to introduce beetles into other conspecific colonies, colonies of a non-host *Cataglyphis* species, and colonies of other genera (*Formica* and *Camponotus*). It was hypothesized that the beetles should have CHC profiles that mimic those of their hosts, which would suggest coevolution.

2. Materials and methods

2.1. The insects

Thorictus martinezi was recently discovered in Burkina Faso (Háva and Lenoir, 2008). The species is associated with a new *Cataglyphis* species belonging to the *bicolor* group (*Cataglyphis* sp. aff. *bicolor* – This species has been provisionally described as *C. lenoiri*, Taylor, 2007). A dozen colonies of this species containing a total of more than 50 beetles were collected in 2006, 2007, and 2008 near Bobo Dioulasso, Burkina Faso (11° 07′01 N; 4° 23′29″ W, 382 m asl). *Thorictus sulcicollis* was collected from *Cataglyphis hispanica* nests near Seville in May 2012 (Spain, Bonares, 37°18′41″ N, 6°41′02″ W, 115 m asl; 3 colonies with a few beetles (Háva and Lenoir, 2010)), and *Thorictus buigasi* was collected from *Cataglyphis viatica* nests in Morocco in May 2012 (Marrakech, 31°41′50.8″ N, 7°59′17.2″ W, 420 m asl, 2 colonies, one with 5 beetles; Ait Ourir, 50 km from Marrakech, 31°32′40″ N, 7°38′55″ W, 710 m asl; 3 colonies with 0, 3, and 15 beetles (Háva and Lenoir, 2010)). The three species belong to the *Thorictus castaneus* group.

Colonies of *Cataglyphis velox* from southern Spain (Torre Quinto near Seville, Andalusia) and *Formica selysi* from south-eastern France (Morillon, Haute-Savoie, located in the Alps) were used in the adoption experiments. *T. buigasi* were also introduced to *Camponotus* nests as Banck (1927) observed one case of *T. foreli* being adopted by *Camponotus ligniperda*; the beetle was attached to the antennae of a worker. We were able to collect one colony of *Camponotus herculeanus* (Morillon, Alps), a sister species of *Camponotus ligniperda*. For the *Cataglyphis* names, we used the feminine as explained in Lenoir et al. (2009).

2.2. Chemical analyses

Whole beetles and ants were used in the chemical analyses. The animals were first frozen at −18 °C for 1 h, then immersed in 200 μL (ants) or 50 μL (beetles) of pentane, and finally stored at −18 °C until the analyses took place. A combined gas chromatography/mass spectrometry system (TurboMass system, PerkinElmer, Norwalk, CT, USA) operating at

70 eV and equipped with a 30-m non-polar DB-5 fused silica capillary column was used. Samples were run using the following temperature program: a 2-min initial hold at 150 °C, a temperature ramp of 5 °C min^{-1} to reach 300 °C, and a 10-min final hold.

The CHC profiles of *Thorictus* species were compared to those of their original and new hosts. Although the ant hydrocarbons had all previously been identified (*Cataglyphis* sp. aff. *bicolor* and *Cataglyphis viatica* in Dahbi et al. (2008), *Cataglyphis hispanica* and *Cataglyphis velox* in Dahbi et al. (1996), and *Formica selysi* in Bagnères et al. (1991). The identities of all of the compounds were verified using their mass spectra and commercial n-alkanes. The hydrocarbon quantity of beetles was also measured using eicosane (C20) as internal standard.

2.3. Behavior and adoption experiments

All ant colonies used in the experiments were reared in large nests. First, the behavior of the beetles in these nests was observed. Second, to examine whether the beetles could be adopted by other *Cataglyphis* colonies or a colony of another species, small experimental colonies of 50–100 workers (see more details in Lenoir et al. (2012)) were used; one beetle was introduced into the foraging arena. The beetle was observed until it was adopted or rejected or for up to 3 days, whichever came first. Adoption was considered to be successful when the beetle remained attached to the antenna of a worker inside the nest for several hours. After 3 days, it was reintroduced into its mother colony or used in chemical analyses. The beetle was considered to be rejected if it spent more than 3 days outside the nest, in the foraging arena. All the beetles were subsequently reintroduced into another host colony, but only after one week had passed. Unfortunately, conducting all of the same adoption experiments with all three species was not possible. Control removals of beetles were also performed: beetles were removed from their mother nests for one to 2 h to verify that they were immediately readopted by the colony without any aggressive behavior on the part of the ants.

2.4. Statistics

Statistical analysis of the chemical profiles was done using all identified peaks. Differences between profiles were explored using cluster analysis (Ward method, Euclidian distances) and Nei distance when it gave more information. Data are presented as the mean ± SE.

3. Results

3.1. Behavior

In the laboratory, *Thorictus* beetles spent several months on the heads of host ant workers; workers carrying beetles (carrier ants) were marked with a dot of paint. Occasionally, the beetles clung to one antenna of a carrier ant for several days before switching to another carrier ant. Carrier ants generally stayed in the nest, but they also went out into the foraging arena carrying the beetle. These observations concurred with field observations, during which some foragers were seen to be carrying beetles. Sometimes a worker seemed to try to expel a beetle with its forelegs, but the attempt only lasted a few minutes. The beetles sometimes disappeared for several days and were probably living in the nest refuse pile. When the beetles were not attached to ants, they roamed freely in the nest and foraging arena. They were observed eating or hiding inside slices of *Tenebrio* larvae that were used to feed the ants. Before attaching themselves to a carrier ant, beetles sometimes exhibited thanatosis behavior (feigning death to evade predation) in the ant's proximity. The worker would seize the beetle with its mandibles, as if it were a prey item or an ant larva, which would provide the beetle with an opportunity to attach to one of the carrier ant's antennae. In *Cataglyphis viatica* nests, *T. buigasi* were frequently found to be attached to alate gynes, a caste preference that may enhance the beetle's dissemination.

Wasmann (1898) suggested that *T. foreli* are haematophagous: they could make small incisions in the antennal cuticle at the level of the scape and suck the "blood" of the host ant. This hypothesis was not supported by Banck (1927). Carrier ants were examined using a binocular microscope and no traces of injury to the cuticle were found. Moreover, in this study, the beetles were observed to feed on insect prey as in Banck (1927), which may explain why Banck found small chitinous items in their digestive tracts.

3.2. Adoption experiments

3.2.1. Thorictus martinezi

Beetle adoption by other *Cataglyphis* sp. aff. *bicolor* colonies from Burkina Faso was very rapid; a maximum of two days passed between the time the beetle entered the nest and was observed on the head of a carrier ant ($n = 10$). A beetle was also introduced into the foraging arena of one *Cataglyphis viatica* nest (a potential allospecific host). The beetle made it to the chamber entrance and even climbed on a worker ($n = 5$), but the worker quickly rejected the beetle, which then remained outside the nest. Of the two beetles introduced into the foraging arena of a *Formica selysi* nest, one died and the other survived for one month outside the nest until the experiment was stopped.

3.2.2. *Thorictus buigasi*

Adoption of *Thorictus buigasi* beetles by *Cataglyphis viatica* nests was very rapid even in heterocolonial nests (4% rejection, Table 1). Beetles were rapidly adopted by *Cataglyphis viatica* colonies that had been collected 50 km from the beetle's colony of origin, most in less than 6 h (5% rejection). The beetles were likewise adopted by allospecific *Cataglyphis velox* colonies from Spain (7% rejection). After adoption, when the beetles were reintroduced into their colonies of origin, some aggression occurred (13% of 34 cases), but it lasted only a few minutes. However, when beetles were introduced into the foraging arena of *F. selysi* colonies, 100% were eventually rejected. In two cases, the beetles entered the host nest without being aggressed and tried, unsuccessfully, to jump on workers. However, they were never observed on host antennae (see photos in Supplementary material), and they returned to the foraging arena after three days and hide in a *Tenebrio* larva corpse. The beetle rejection rate was therefore considered to be 100%. Surprisingly, 50% of *T. buigasi* were adopted by *Camponotus herculeanus* colonies, and thus adoption was partially successful (see photos).

3.3. Chemical profiles of the beetles and their hosts

The chromatograms of *Cataglyphis viatica* and *Thorictus buigasi* are similar (Fig. 1). They both contain the same hydrocarbon profile, a pattern that indicates chemical mimicry even if some quantitative differences are present. *Thorictus buigasi* has more saturated hydrocarbons than its ant host (30% vs. 19%, Table S1). *Cataglyphis velox* has the same hydrocarbons as *Cataglyphis viatica*, although there are some quantitative differences (Fig. 2). This analysis did not detect any compounds that could be considered to be produced by trichomes. This result contrasts with that of Banck (1927) and reflects differences in the methods used.

The hydrocarbon profiles of individual *Cataglyphis viatica*, *Cataglyphis velox*, and *T. buigasi* (taken from its original host *C. viatica* or from a *C. velox* nest after adoption) were compared as well (Fig. 3). The comparison shows that *C. viatica* and *C. velox* have different CHC profiles (Nei = 0.65 ± 0.01, $n = 60$) and that the beetles partially retained a chemical identity independent of that of the host (only one aggregated with the host = ThVia5; Nei distance between *C. viatica* and *T. buigasi* was 0.66 ± 0.02, $n = 54$). When the beetles were adopted by a *C. velox* colony, they also retained their identity relative to that of the new host after 3 days (Nei = 0.70 ± 0.06, $n = 15$, which does not differ from the pre-adoption profile in *C. viatica* colonies: Nei = 0.79 ± 0.02, $n = 18$).

In *Thorictus buigasi*, hydrocarbon quantity averaged 75 ng/beetle (SE 14.6, $n = 12$).

A broader comparison of species was also conducted using the mean profiles of each species sampled (Fig. 4). This comparison shows that the profiles of *C. velox* and *C. viatica* are similar to those of other *Cataglyphis* species and that *Thorictus buigasi* is most similar to its host species *C. viatica* or its species of adoption *C. velox*, even if its profile is also distinctly different. Likewise, the CHC profiles of the other two beetle species matched those of their respective hosts (*T. sulcicollis*/*Cataglyphis hispanica*: 0.66 ± 0.03, $n = 20$, Fig. S1; *T. martinezi*/*Cataglyphis* sp. aff. *bicolor* 0.77 ± 0.02, $n = 59$, Fig. S2). Moreover, the three *T. buigasi* beetles adopted by *Camponotus herculeanus* presented CHCs that completely matched those of their new host (0.94 ± 0.01, $n = 9$, Fig. S3). They more or less completely lost some methyl hydrocarbons (Table S1: 3C25: declined from 1.97% to 0%; 3,9C25 declined from 3.75% to 0%; 3C27 declined from 10.82% to 0%; 3,7C27 declined from 14.18% to 3.56%–0.41%; 10C28 declined from 3.78% to 0%) and gained others (7,11C29 increased from 0% to 24.5%). This result indicates that the beetles probably mimic their host using camouflage. The CHC profile of *Formica selysi* was completely different from those of all the other ant and beetle species and was characterized by an abundance of alkenes (90%; table S1); this chemical disparity may explain the inability of the beetles to be adopted by this species.

4. Discussion

All the beetles of the *Thorictus castaneus* group are myrmecophiles, and they remain attached to the heads of their hosts. *T. buigasi* beetles are characterized by small quantities of hydrocarbons (75 ng) compared to other myrmecophile genera such as *Sternocoelis*, which averages 450 ng per beetle of the same size (Lenoir et al., 2012). They can, therefore, be considered to be at least partly "insignificant", as per Lenoir et al. (1999). This chemical insignificance may explain why the beetles were never the target of aggression when they tried to enter the nest of a very different host, such as *Formica* or *Camponotus*. However, the three *Thorictus* species nonetheless had enough cuticular hydrocarbons to chemically match and thus mimic their hosts.

Table 1
Number of successful adoptions of *Thorictus buigasi* inquilines by conspecific host colonies, congeneric non-host colonies, and colonies of other genera.

Adoptive colony	Adoption<6 h	Adoption>6 h	Adoption>24 h	Rejected	% Rejected	*n*
Cataglyphis viatica – same site intercolonial	20	3	0	1	4.2	24
Cataglyphis viatica – different site same species	18	1	0	1	5.0	20
Cataglyphis velox	12	1	0	1	7.1	14
Formica selysi	0	0	0	12	100[a]	12
Camponotus herculeanus	0	0	3	3	50[b]	6

[a] Two were initially adopted but exited the nest after 3 days.
[b] One died after 2 days.

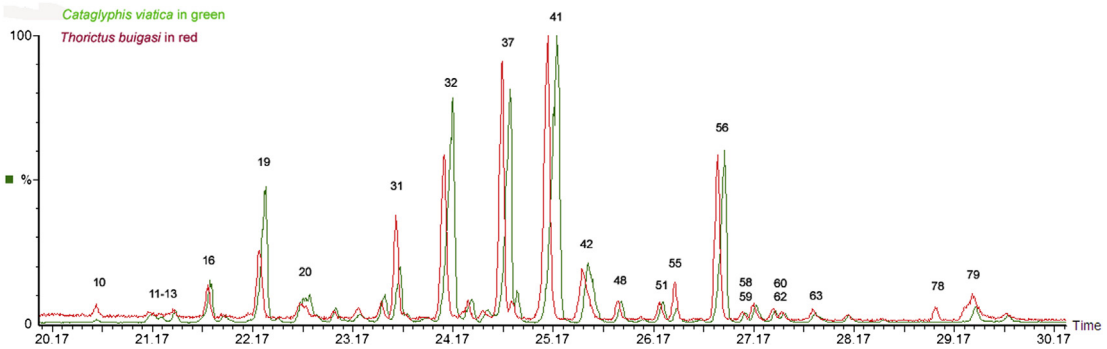

Fig. 1. Gas chromatograms of the CHCs of *Thorictus buigasi* (in red) and *Cataglyphis viatica* (in green). Chromatograms are deliberately not completely superimposed. Peak numbers refer to the hydrocarbons described in Table S1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Nevertheless, they partially maintained their chemical identity; they were not subject to aggressive behavior but were probably also recognized as being different from the ant workers. This chemical difference can be compared to that observed between slaves and slave-makers, which has been described for mixed colonies of *Formica/Polyergus* (D'ettorre et al., 2002) or *Proformica/Rossomyrmex* (Zamora-Munoz et al., 2003).

Thorictus beetles, and other myrmecophilous taxa, demonstrate two life history patterns with regards to their ant hosts. They can be generalists, like *T. grandicollis*, and live in the nests of various, very different ant species. They can also be specialists, like *T. foreli* and *T. buigasi*, and live in the nests of only one host species. Generalist *Thorictus* species display characteristic appeasement behavior when handled by ants and do not jump on the host's antennae (Cammaerts and Cammaerts, 1994). Parasitic *Formicoxenus nitidulus* are able to live in the nests of many different host species and switch between them, and they do not chemically mimic their hosts (Lenoir et al., 2001; Martin et al., 2008). It will be interesting to study the mimicry of generalist *Thorictus* species. Myrmecophilous crickets (*Myrmecophilus* spp.) also vary in their behavior and can be either generalists or specialists (Akino et al., 1996; Komatsu et al., 2009, 2013).

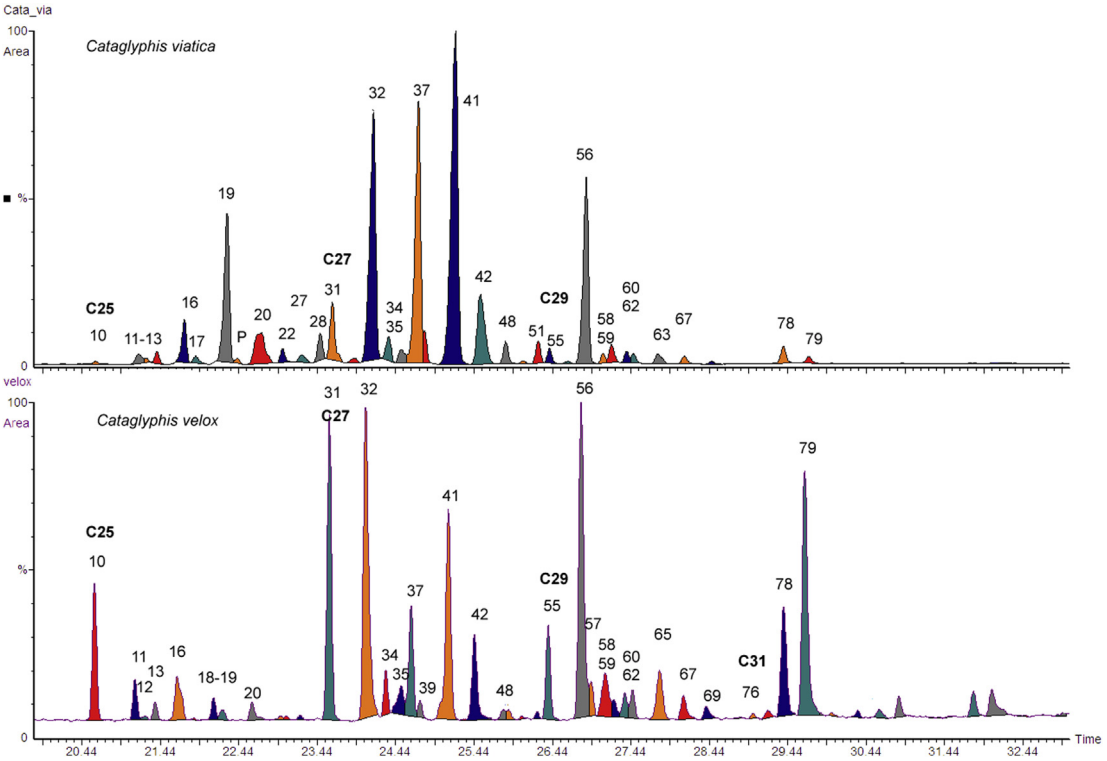

Fig. 2. Gas chromatograms of the CHCs of *Cataglyphis viatica* and *Cataglyphis velox*. Peak numbers refer to the hydrocarbons described in Table S1.

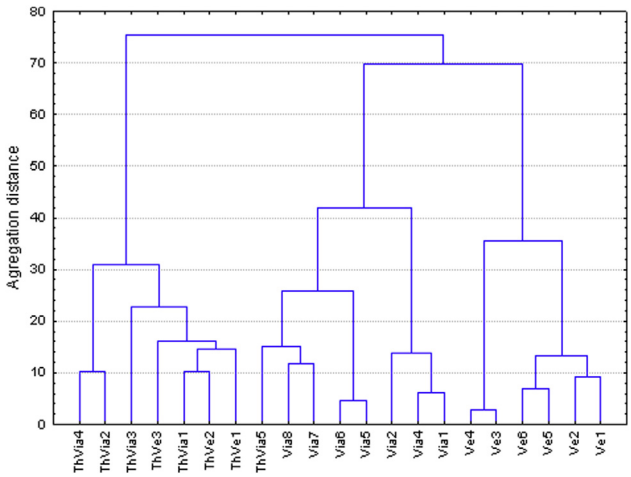

Fig. 3. Dendrogram of the CHC profiles of *Cataglyphis viatica* and *Cataglyphis velox* and their guest *Thorictus buigasi* (Ward method, Euclidian distances). Via = *Cataglyphis viatica*; Ve = *Cataglyphis velox*; ThVia = *Thorictus buigasi* in *C. viatica* nest; ThVe = *T. buigasi* in *C. velox* nest after adoption.

Some *Cataglyphis* specialists like *T. foreli* are well known (Wasmann, 1898), yet aspects of their ecology remain unknown. For instance, phoretic *Thorictus* may be costly for the ants, who try to expel them. Wasmann (1898) suggested that *T. foreli* beetles are haematophagous: they could make small incisions at the scape level of the antennal cuticle and suck the "blood" of the host ant. However, this hypothesis was not supported by Banck (1927). The beetle species studied here are *Cataglyphis* specialists, and the chemical similarity between the beetles and their host species suggests chemical coevolution. This interpretation is supported by the observation that beetles originating from *Cataglyphis viatica* nests were readily adopted by *Cataglyphis velox* nests, apparently because of the similarity in CHC profiles between the two hosts. A similar response might occur if *T. martinezi* were to be adopted by a different species of *Cataglyphis bicolor* group as the CHCs of both species are similar. It is proposed that the beetles synthesize host hydrocarbons in small quantities to sufficiently match their host's profile, an approach that has recently been observed in *Sternocoelis* beetles that live in *Aphaenogaster senilis* colonies (Lenoir et al., 2012). However, the fact that the beetles were adopted by *Camponotus herculeanus*, a non-congeneric species, and were able to conform to the new host's CHC profile indicates that some plasticity exists in the beetle's chemical signature. We did not try to introduce the beetles into colonies of *Cataglyphis hispanica*, a species that is intermediate to *Cataglyphis viatica* and *Camponotus herculeanus*. Their chemical plasticity is nonetheless limited because adoption appears to be impossible when the new host is too different, as in the case of *F. selysi*, whose CHCs were mainly alkenes. Morphological as well as chemical characters could restrict the ability of these beetles to exploit different and distant species. For example, beetles could find

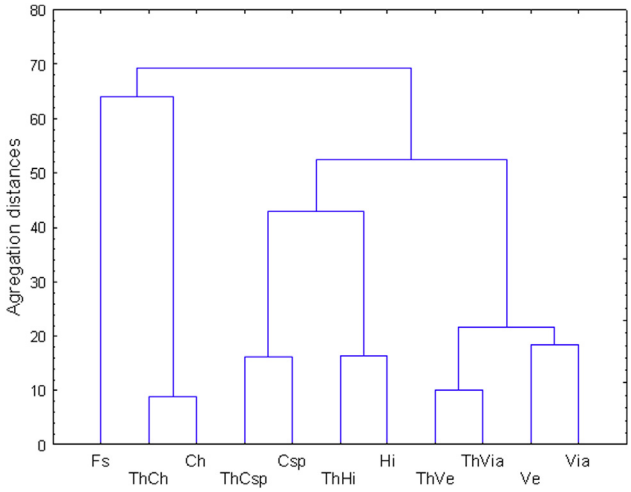

Fig. 4. Dendrogram of the CHCs profiles of ants and their guests (Ward method, Euclidian distances). Each point is the mean for the samples. Via = *Cataglyphis viatica*; Ve = *Cataglyphis velox*; ThVia = *Thorictus buigasi* in *C. viatica* nest; ThVe = *T. buigasi* in *C. velox* nest; Hi = *Cataglyphis hispanica*; ThHi = *T. sulcicollis* in *C. hispanica* nest; Csp = *Cataglyphis* sp. aff. *bicolor* (from Burkina Faso); ThCsp = *T. martinezi* in *C.* sp. aff. *bicolor* nest; Fs = *Formica selysi*; Ch = *Camponotus herculeanus*, ThCh = *T. buigasi* in *C. herculeanus* nest.

difficult to cling to carrier ants, maybe due to differences in the morphology of the ant's antennae or head or differences in body size. Ant species may differ in their grooming activities, with some species being more effective at removing beetles than others. Future research is needed to determine whether beetles synthesize their CHCs themselves or acquire them from their hosts. To do so, it will be necessary to measure the CHC levels of isolated beetles. If the beetles synthesize their own CHCs, levels should be maintained over time; however, if they acquire them, then levels should decrease in the absence of contact with their host. More samples are needed to study this pattern.

Acknowledgments

We particularly thank Jean-Marie Martinez for collecting ant colonies in Burkina Faso, Jean-Philippe Christidès for maintaining the GC-MS and helping with the chemical analyses, and Guy Bourdais for maintaining the ant colonies. Thanks to Karine Poitrineau for her translation of the Reichensperger paper, Jessica Pearce for the English revision and reviewers for their constructive comments.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.bse.2013.10.002.

References

Akino, T., 2008. Chemical strategies to deal with ants: a review of mimicry, camouflage, propaganda, and phytomimesis by ants (Hymenoptera: Formicidae) and other arthopods. Myrmecol. News 11, 173–181.
Akino, T., Mochizuki, R., Morimoto, M., Yamaoka, R., 1996. Chemical camouflage of myrmecophilous cricket *Myrmecophilus* sp. to be integrated with several ant species. Jpn. J. Appl. Entomol. Zool. 40, 39–46.
Bagnères, A.-G., Errard, C., Mulheim, C., Joulie, C., Lange, C., 1991. Induced mimicry of colony odors in ants. J. Chem. Ecol. 17, 1641–1664.
Bagnères, A.-G., Lorenzi, M.C., 2010. Chemical deception/mimicry using cuticular hydrocarbons. In: Blomquist, G.J., Bagnères, A.-G. (Eds.), Insect Hydrocarbons: Biology, Biochemistry and Chemical Ecology. Cambridge University Press, pp. 282–323.
Banck, L.J., 1927. An Anatomical – Histological and Experimental – Biological Study of *Thorictus Foreli* Wasm. PhD. University of Fribourg, Switzerland,.
Cammaerts, R., Cammaerts, M.C., 1994. Supragenericc taxonomy, appeasement behavior, sex ratio and other aspects of the biology of the myrmecophilous beetle *Thorictus grandicollis* (Dermestidae, Thorictinae). Bull. Ann. Soc. Roy. Entomol. Belg. 130, 203–230.
Cristaldo, P., Rosa, C., Florencio, D., Marins, A., Desouza, O., 2012. Termitarium volume as a determinant of invasion by obligatory termitophiles and inquilines in the nests of *Constrictotermes cyphergaste*r (Termitidae, Nasutitermitinae). Insectes Soc. 59, 541–548.
D'ettorre, P., Lenoir, A., 2010. Nestmate recognition in ants. In: Lach, L., Parr, C., Abbott, K. (Eds.), Ant Ecology. Oxford University Press, Oxford, pp. 194–209.
D'ettorre, P., Mondy, N., Lenoir, A., Errard, C., 2002. Blending on with the crowd: social integration into their host colonies using a flexible signature. Proc. R. Soc. Lond. B 269, 1911–1918.
Dahbi, A., Hefetz, A., Lenoir, A., 2008. Chemotaxonomy of some *Cataglyphis* ants from Morocco and Burkina Faso. Biochem. Syst. Ecol. 36, 564–572.
Dahbi, A., Lenoir, A., Tinaut, A., Taghizadeh, T., Francke, W., Hefetz, A., 1996. Chemistry of the postpharyngeal gland secretion and its implication for the phylogeny of Iberian *Cataglyphis* species (Hymenoptera: Formicidae). Chemoecol. 7, 163–171.
Endo, S., Itino, T., 2013. Myrmecophilous aphids produce cuticular hydrocarbons that resemble those of their tending ants. Popul. Ecol. 55, 27–34.
Háva, H., Lenoir, A., 2008. *Thorictus martinezi*, sp. n. from Burkina Faso (Coleoptera: Dermestidae: Thorictini). Calodema. Suppl. 5 pp. Paper 77.
Háva, H., Lenoir, A., 2010. *Thorictus sulcicollis* Pérez Arcas, 1868 (Coleoptera: Dermestidae: Thorictini), new data from Spain. Arquiv. Entomol. 4, 3–4.
Hefetz, A., 2007. The evolution of hydrocarbon pheromone parsimony in ants (Hymenoptera: Formicidae) – interplay of colony odor uniformity and odor idiosynchrasy. Myrmecol. News 10, 59–68.
Hölldobler, B., Wilson, E.O., 1990. The Ants. The Belknap Press, Cambridge, p. 782.
Howard, R.H., Mcdaniel, C.A., Blomquist, G.J., 1982. Chemical mimicry as an integrating mechanism for three termitophiles associated with *Reticulitermes virginicus* (Banks). Psyche 89, 157–167.
Howard, R.W., Mcdaniel, C.A., Blomquist, G.J., 1980. Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. Science 210, 431–433.
Kistner, D.H., 1979. In: Hermann, H.R. (Ed.), Social and Evolutionary Significance of Social Insect Symbionts, Social Insects, vol. 1. Academic Press, New York, pp. 339–413, 437 p.
Komatsu, T., Maruyama, M., Itino, T., 2009. Behavioral differences between two ant cricket species in Nansei islands: host-specialist versus host-generalist. Insectes Soc. 56, 389–396.
Komatsu, T., Maruyama, M., Itino, T., 2013. Non-integrated host-association of *Myrmecophilus tetramorii*, a specialist myrmecophilous ant cricket (Orthoptera: Myrmecophilidae). Psyche 2013, 5. Article ID 568536.
Kronauer, D.J.C., Pierce, N.E., 2011. Myrmecophiles. Curr. Biol. 21, R208–R209.
Lenoir, A., Aron, S., Cerdá, X., Hefetz, A., 2009. *Cataglyphis* desert ants: a good model for evolutionary biology in the Darwin's anniversary year. Isr. J. Entomol. 39, 1–32.
Lenoir, A., Chalon, Q., Carvajal, A., Ruel, C., Barroso, Á., Lackner, T., Boulay, R., 2012. Chemical integration of myrmecophilous guests in *Aphaenogaster* ant nests. Psyche, 12. Article ID 840860.
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., Fresneau, D., Errard, C., Hefetz, A., 1999. The individuality and the colonial identity in ants: the emergence of the social representation concept. In: Detrain, C., Deneubourg, J.L., Pasteels, J. (Eds.), Information Processing in Social Insects. Birkhäuser Verlag, Basel, pp. 219–237.
Martin, S.J., Takahashi, J.-I., Ono, M., Drijfhout, F.P., 2008. Is the social parasite *Vespa dybowskii* using chemical transparency to get her eggs accepted? J. Insect Physiol. 15, 700–707.
Reichensperger, A., 1925. Beobachtungen und Versuche mit *Cataglyphis* und *Thorictus* nebst dessen Metamorphose. Beschreibung zweier neuer Myrmekophilen. Verh. Nat. Hist. Ver. (Bonn) 82, 73–111.
Sanchez-Pinero, F., Gomez, J.M., 1995. Use of ant-nest debris by darkling beetles and other arthropod species in an arid system in south Europe. J. Arid Environ. 31, 91–104.
Schmid-Hempel, P., 1998. Parasites in Social Insects. Princeton University Press, Princeton, p. 409.
Stoeffler, M., Tolasch, T., Steidle, J., 2011. Three beetles three concepts. Different defensive strategies of congeneric myrmecophilous beetles. Behav. Ecol. Sociobiol. 65, 1605–1613.
Taylor, B., 2007. The Ants of Africa. http://antsofafrica.org.
Von Beeren, C., Schulz, S., Hashim, R., Witte, V., 2011. Acquisition of chemical recognition cues facilitates integration into ant societies. BMC Ecol. 11, 30.
Wasmann, E., 1898. *Thorictus Foreli* als Ectoparasit der Ameisenfühler. Zool. Anz. 21, 435–436.

Wheeler, W.M., 1910. Ants: Their Structure, Development and Behavior, fourth printing 1965, vol. xxv. Columbia University Press, New York, p. 663.
Wilson, E.O., 1971. The Insect Societies. Harvard University Press, Cambridge, MA, p. 548.
Witte, V., Leingärtner, A., Sabaß, L., Hashim, R., Foitzik, S., 2008. Symbiont microcosm in an ant society and the diversity of interspecific interactions. Anim. Behav. 76, 1477–1486.
Zamora-Munoz, C., Ruano, F., Errard, C., Lenoir, A., Hefetz, A., Tinaut, A., 2003. Coevolution in the slave-parasite system *Proformica longiseta – Rossomyrmex minuchae* (Hymenoptera: Formicidae). Sociobiol. 42, 299–317.

Supplementary data - Lenoir et al. (2013) Chemical integration of Thorictus myrmecophilous beetles into Cataglyphis ant nests. Biochemical Systematics and Ecology 51: 335-342.

Table S1.Composition of ant and Thorictus beetle cuticular hydrocarbons (means ± SE).

Peak	Name	C. viatica		Th buigasi Tb		C. herculeanus Ch		Tb / Ch		Formica selysi	
n°		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
1	C23:1									0.27	*0.13*
2	C23	0.07	*0.04*			**7.27**	*1.26*	3.86	*0.39*	0.84	*0.18*
3	9+11C23					0.17	*0.04*	0.11	*0.06*	0.12	*0.03*
4	5C23									0.03	*0.02*
5	3C23									0.11	*0.02*
6	C24	0.31	*0.14*	0.52	*0.32*	**5.17**	*0.37*	2.31	*0.48*	0.07	*0.04*
7	5C24					0.30	*0.04*	0.17	*0.14*		
8	4C24	0.14	*0.06*	0.10	*0.09*						
9	C25:1	0.06	*0.04*							2.30	*0.25*
10	C25	1.71	*0.43*	0.98	*0.11*	**6.51**	*0.81*	2.66	*0.64*	4.32	*1.17*
11	9+11+13C25	0.64	*0.08*	**5.28**	*3.65*	2.80	*0.65*	2.96	*0.17*	0.31	*0.03*
12	7C25	0.08	*0.04*	0.06	*0.04*	0.46	*0.12*	0.30	*0.22*	0.06	*0.06*
13	5C25	0.70	*0.08*	0.86	*0.23*	0.30	*0.30*			0.08	*0.06*
14	C12:C12 Ester										
15	C26:1	0.04	*0.02*							0.71	*0.05*
16	3C25	2.79	*0.44*	1.97	*0.60*					0.00	*0.00*
17	5,9+7,9C25	0.19	*0.05*	0.03	*0.03*					0.02	*0.02*
18	C26	1.27	*0.38*	0.05	*0.05*	2.21	*0.18*	0.87	*0.28*	0.11	*0.04*
19	3,7+3,9+3,13C25	4.61	*0.74*	3.75	*0.66*						
20	10+11+12+13 C26	1.35	*0.44*	0.59	*0.36*	1.45	*0.24*	1.47	*0.17*		
21	6C26	0.04	*0.02*								
22	4C26	0.56	*0.09*	0.09	*0.09*	0.12	*0.12*				
23	10,12+10,14+12,16C26	0.03	*0.02*								
24	C27:2									0.05	*0.05*
25	C27:2									0.37	*0.28*
26	C27:2									2.48	*1.63*
27	6,10C26	0.22	*0.11*	0.16	*0.16*						
28	4,8+4,10C26	0.47	*0.22*	0.20	*0.20*						
29	C27:1	0.45	*0.21*							**32.31**	*4.95*
30	4,10C26	0.05	*0.02*								
31	C27	**9.76**	*1.72*	**5.07**	*0.81*	2.38	*0.19*	1.33	*0.60*	3.77	*1.00*
32	9+11+13C27	**10.73**	*1.22*	**8.11**	*1.12*	**13.26**	*1.23*	**13.67**	*1.52*	0.67	*0.21*
33	7C27	0.04	*0.04*	0.14	*0.08*	4.59	*0.27*	5.67	*0.38*	0.00	*0.00*
34	5C27	1.33	*0.19*	1.10	*0.16*	4.65	*0.19*	4.55	*0.51*	0.26	*0.05*
35	11,15+13,15C27	0.88	*0.25*	0.47	*0.18*						
36	9,11+7,11+9,13C27	0.59	*0.54*	0.00	*0.00*						
37	3C27	**16.83**	*1.29*	**10.82**	*1.19*						
38	C28:1									0.58	*0.25*
39	5,9+5,11C27	0.29	*0.18*	0.20	*0.20*					0.22	*0.11*
40	C28	1.46	*0.68*	0.00	*0.00*	0.46	*0.12*			0.06	*0.01*
41	3,7+3,9C27	**11.33**	*2.84*	**14.18**	*2.18*	0.41	*0.10*	3.56	*1.46*		
42	10+11+12+14C28	4.88	*0.37*	3.78	*0.68*						
43	12C28+11,13,15C27										
44	C29:2									2.29	*2.29*
45	C29:2									**14.89**	*5.15*
46	C29:2									**9.00**	*1.00*
47	11,15,17+13,15,17C27	1.78	*0.50*	0.58	*0.36*						
48	4C28	0.96	*0.16*	0.78	*0.28*						
49	C29:1									**11.98**	*5.45*
50	C29:1	0.31	*0.15*								
51	4,8+4,10C28	0.13	*0.06*			0.92	*0.09*	0.42	*0.37*		
52	3MeC28:1										
53	C29:1	0.15	*0.06*								
54	4,10+4,12C28	0.67	*0.15*	0.97	*0.10*						
55	C29	2.71	*0.66*	**9.48**	*2.48*	0.47	*0.13*	2.77	*1.23*	0.96	*0.36*
56	9+11+13+15C29	**10.09**	*0.92*	**7.20**	*0.98*	**8.18**	*0.42*	**10.18**	*1.04*	0.34	*0.18*
57	7C29										
58	5C29	0.70	*0.11*	0.85	*0.27*						
59	11,15+13,15C29	1.20	*0.27*	0.44	*0.27*						
60	3C29	1.23	*0.23*	1.53	*0.22*						
61	7,11+7,15+7,17C29					**23.19**	*2.17*	**24.50**	*3.93*		
62	5,9+5,11C29	0.23	*0.09*	0.29	*0.18*	1.62	*0.34*	2.77	*0.44*		
63	C30	0.88	*0.17*	2.41	*0.53*	0.40	*0.10*	1.03	*0.67*		
64	3,9C29					0.91	*0.24*	0.96	*0.06*		
65	8+10+12+13+14+15C30	0.31	*0.10*								

Peak	Name	C. viatica		Th buigasi Tb		C. herculeanus Ch		Tb / Ch		Formica selysi	
n°		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
66	8C30					0.99	*0.25*	0.39	*0.19*		
67	11,13,15+13,15,17C29	0.15	*0.07*	0.17	*0.11*						
68	10,16+12,14C30										
69	4C30	0.18	*0.05*	0.13	*0.09*						
70	C31:2									0.53	*0.53*
71	C31:2									**6.79**	*3.48*
72	6,10+8,12C30										
73	C31:1									2.03	*1.20*
74	4,10+4,12C30										
75	C31:1										
76	C31	0.35	*0.17*	11.41	*3.60*			3.71	*1.57*		
77	MeC31:1										
78	9+11+13+15C31	1.35	*0.24*	3.05	*0.99*	0.73	*0.12*	1.17	*0.55*	0.15	*0.10*
79	11,13+11,15+13,15+13,17C31	1.06	*0.24*	0.45	*0.18*						
80	7C31					4.58	*0.63*	**5.15**	*1.27*		
81	5C31					0.85	*0.18*	1.03	*0.52*		
82	9,13+9,17C31										
83	7,11+7,15C31										
84	5,9+5,11C31	0.01	*0.01*	0.02	*0.02*						
85	3MeC31										
86	C32	0.15	*0.08*	0.10	*0.10*						
87	5,9,13+5,11,15C31					0.52	*0.15*	0.98	*0.56*		
88	10+11+12+13+14C32	0.09	*0.02*								
89	6+7+8C32										
90	11,13+13,17C32	0.06	*0.03*								
91	C33:2									1.02	*0.69*
92	12,14+12,16C32 +14,18C32										
93	6,12+8,12+8,16C32	0.01	*0.01*	0.05	*0.05*						
94	C33:1										
95	C33:1									0.09	*0.09*
96	C33	0.07	*0.04*	0.33	*0.21*						
97	15+17C33:1										
98	9+11+13+15+17C33	0.22	*0.05*	0.25	*0.14*					0.03	*0.03*
99	11,15+13,15+13,17C33	0.56	*0.16*	0.26	*0.11*	0.33	*0.16*	0.20	*0.20*		
100	13,x+15,xC33										
101	7,11+7,15C33					1.23	*0.60*	0.70	*0.35*		
102	3C33										
103	5,xC33					0.11	*0.11*				
104	C34	0.04	*0.02*			0.04	*0.04*				
105	11+12+13+14+15+17C34	0.01	*0.01*								
106	C35:1										
107	15C35:1										
108	13,17+15,17C34	0.04	*0.02*								
109	3+4+5C34					0.29	*0.07*	0.04	*0.04*		
110	15C35:1										
111	C35:1					0.02	*0.02*			0.05	*0.05*
112	C35	0.01	*0.01*								
113	9+11+13+15+17C35	0.07	*0.02*	0.05	*0.05*	0.42	*0.12*	0.06	*0.06*		
114	11,15+13,15+15,17+17,19C35	0.29	*0.08*	0.69	*0.20*						
115	11,xC35					0.96	*0.33*	0.46	*0.29*		
116	7,11C35										
117	C36	0.01	*0.01*			0.12	*0.12*				
118	11+12+13+14C36					0.13	*0.13*				
119	8C36					0.06	*0.06*				
120	C37:1										
121	C37					0.08	*0.08*				
122	13+15+17C37					0.01	*0.01*				
123	11,x+13,x+15,xC37										
124	C38					0.15	*0.15*				
125	Di MeC39					0.04	*0.04*				
	Total n-alKanes	18.82	*3.57*	30.35	*6.75*	25.26	*1.98*	18.54	*5.07*	10.14	*2.45*
	Total alkenes	1.02	*0.36*	0.00	*0.00*	0.02	*0.02*	0.00	*0.00*	**87.47**	*2.22*
	Total methyl-alkanes	80.16		69.65		74.72		81.46		2.39	
	n=	11		5		5		3		3	
	In bold % > 5%, in red alkenes in F selysi										

Peak	Name	C. velox		Tb / C. velox		C. hispanica		T sulcicollis		C. sp		T martinezi	
n°		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
1	C23:1											0.91	*0.79*
2	C23	0.06	*0.03*			1.20	*0.51*					0.23	*0.20*
3	9+11C23												
4	5C23												
5	3C23												
6	C24	0.20	*0.06*	0.05	*0.05*	1.06	*0.79*					0.09	*0.08*
7	5C24												
8	4C24	0.01	*0.01*	0.05	*0.05*								
9	C25:1	0.01	*0.01*	0.00	*0.00*	0.25	*0.09*			0.31	*0.20*	0.02	*0.02*
10	C25	**8.45**	*1.66*	4.54	*2.06*	6.31	*2.04*	3.20	*1.62*	0.41	*0.27*	0.84	*0.56*
11	9+11+13C25	1.42	*0.33*	**6.49**	*0.11*	4.00	*0.70*	0.75	*0.35*	0.09	*0.05*	0.05	*0.06*
12	7C25	0.13	*0.06*			0.41	*0.33*	0.69	*0.26*	0.02	*0.02*		
13	5C25	1.65	*0.99*	2.10	*0.28*	0.42	*0.42*	1.92	*1.18*	0.47	*0.33*	0.15	*0.10*
14	C12:C12 Ester									0.55	*0.36*	0.03	*0.03*
15	C26:1	0.00	*0.00*	0.00	*0.00*	0.00	*0.00*						
16	3C25	**5.33**	*2.56*	1.97	*1.61*	0.61	*0.17*	0.61	*0.34*				
17	5,9+7,9C25					0.55	*0.13*	0.30	*0.12*				
18	C26	1.50	*0.25*			0.76	*0.13*	0.27	*0.13*	0.12	*0.04*	0.36	*0.12*
19	3,7+3,9+3,13C25	0.54	*0.15*	2.04	*1.02*	0.34	*0.10*	0.56	*0.46*				
20	10+11+12+13 C26	0.76	*0.21*	4.10	*1.75*	1.22	*0.19*	0.24	*0.14*	0.37	*0.23*	0.13	*0.09*
21	6C26												
22	4C26	0.36	*0.16*							0.07	*0.04*	0.69	*0.41*
23	10,12+10,14+12,16C26												
24	C27:2												
25	C27:2												
26	C27:2												
27	6,10C26												
28	4,8+4,10C26												
29	C27:1					0.86	*0.11*	0.15	*0.10*				
30	4,10C26												
31	C27	**12.11**	*0.84*	**6.82**	*1.15*	4.16	*0.69*	2.31	*0.78*	0.54	*0.10*	4.43	*1.62*
32	9+11+13C27	**9.84**	*1.23*	**11.35**	*1.07*	**5.34**	*0.56*	1.35	*1.08*	1.24	*0.35*	2.64	*1.45*
33	7C27	0.06	*0.06*							0.33	*0.21*	0.26	*0.17*
34	5C27	1.88	*0.19*	1.78	*1.08*	0.11	*0.11*	0.46	*0.19*	0.82	*0.52*	0.26	*0.12*
35	11,15+13,15C27	1.02	*0.40*	0.44	*0.44*					0.30	*0.18*	0.54	*0.29*
36	9,11+7,11+9,13C27	0.12	*0.12*	0.00	*0.00*	0.52	*0.52*						
37	3C27	3.49	*0.16*	**7.48**	*0.61*	1.72	*0.48*	0.98	*0.28*	1.59	*0.33*	1.73	*0.68*
38	C28:1												
39	5,9+5,11C27	0.29	*0.13*			0.45	*0.10*	0.37	*0.07*				
40	C28	0.08	*0.08*							0.27	*0.06*	0.69	*0.26*
41	3,7+3,9C27	**7.16**	*0.50*	**11.27**	*0.24*	4.35	*2.35*	3.61	*1.94*	0.64	*0.03*	0.15	*0.13*
42	10+11+12+14C28	2.69	*0.23*	**5.27**	*1.57*	2.11	*0.50*	1.06	*0.45*	1.63	*0.32*	0.94	*0.58*
43	12C28+11,13,15C27									0.98	*0.40*	0.81	*0.58*
44	C29:2												
45	C29:2												
46	C29:2												
47	11,15,17+13,15,17C27	0.08	*0.08*							0.25	*0.16*	0.29	*0.29*
48	4C28	0.75	*0.15*	0.63	*0.63*					0.33	*0.04*	0.82	*0.32*
49	C29:1												
50	C29:1												
51	4,8+4,10C28									0.27	*0.05*		
52	3MeC28:1									0.13	*0.06*	0.05	*0.05*
53	C29:1	0.12	*0.07*			0.39	*0.26*			0.10	*0.03*		
54	4,10+4,12C28	0.33	*0.11*	2.34	*1.72*								
55	C29	4.02	*0.40*	**9.20**	*0.87*	2.55	*0.35*	2.95	*0.87*	**6.92**	*1.29*	11.11	*2.22*
56	9+11+13+15C29	**9.63**	*1.00*	**6.22**	*1.29*	**8.78**	*0.82*	3.53	*0.49*	**29.83**	*1.24*	20.46	*4.35*
57	7C29	0.19	*0.19*							0.23	*0.10*	0.62	*0.18*
58	5C29	2.51	*0.26*	0.24	*0.24*	0.27	*0.20*	0.05	*0.05*	1.28	*0.15*	1.01	*0.24*
59	11,15+13,15C29	0.14	*0.08*							0.75	*0.13*	0.29	*0.20*
60	3C29	1.37	*0.27*					1.65	*1.53*	**7.37**	*0.70*	6.74	*1.19*
61	7,11+7,15+7,17C29					1.02	*0.16*	0.64	*0.35*				
62	5,9+5,11C29	1.07	*0.28*			1.66	*0.26*	2.39	*1.42*	0.01	*0.01*	0.51	*0.45*
63	C30	0.94	*0.44*	1.71	*0.86*	0.46	*0.17*	1.69	*0.38*				
64	3,9C29					0.46	*0.25*	1.08	*0.19*				
65	8+10+12+13+14+15C30	1.93	*0.50*			0.79	*0.26*	2.09	*1.52*	4.34	*1.85*	2.48	*1.72*

Peak	Name	C. velox		Tb / C. velox		C. hispanica		T sulcicollis		C. sp		T martinezi	
n°		mean	SE	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
66	8C30					0.09	*0.09*			7.07	*1.31*	5.26	*1.64*
67	11,13,15+13,15,17C29	0.58	*0.26*										
68	10,16+12,14C30	0.79	*0.60*							3.36	*0.25*	1.40	*0.75*
69	4C30	0.13	*0.13*							0.59	*0.17*	1.27	*0.85*
70	C31:2												
71	C31:2												
72	6,10+8,12C30					0.12	*0.12*			0.35	*0.16*	0.05	*0.05*
73	C31:1	0.02	*0.02*							0.62	*0.18*	0.00	*0.00*
74	4,10+4,12C30									0.09	*0.07*	0.14	*0.12*
75	C31:1									1.10	*0.48*	0.04	*0.05*
76	C31	0.32	*0.06*	6.33	*0.67*	0.09	*0.09*	2.63	*1.25*	0.42	*0.07*	7.63	*4.06*
77	MeC31:1									1.84	*0.55*	1.39	*0.78*
78	9+11+13+15C31	4.11	*0.23*	**5.28**	*2.52*	**10.55**	*2.44*	**9.97**	*3.10*	**15.64**	*1.92*	**8.73**	*2.35*
79	11,13+11,15+13,15+13,17C31	**7.17**	*1.16*	1.34	*0.63*	0.29	*0.29*			2.17	*0.53*	1.98	*0.58*
80	7C31												
81	5C31									0.60	*0.13*	0.09	*0.06*
82	9,13+9,17C31									0.17	*0.08*		
83	7,11+7,15C31	0.08	*0.08*			**5.99**	*1.65*	18.17	*2.38*				
84	5,9+5,11C31	0.04	*0.04*			0.79	*0.07*	3.13	*0.39*	0.67	*0.10*		
85	3MeC31									0.27	*0.12*	0.05	*0.06*
86	C32	0.17	*0.08*			0.14	*0.14*						
87	5,9,13+5,11,15C31					0.00	*0.00*						
88	10+11+12+13+14C32	0.54	*0.08*			1.32	*0.22*	3.00	*0.66*			0.19	*0.17*
89	6+7+8C32									0.31	*0.15*	0.41	*0.28*
90	11,13+13,17C32	0.20	*0.13*										
91	C33:2												
92	12,14+12,16C32 +14,18C32	0.57	*0.30*							0.16	*0.09*	0.29	*0.25*
93	6,12+8,12+8,16C32	0.15	*0.15*			1.62	*0.34*	3.51	*0.43*	0.15	*0.04*		
94	C33:1					0.07	*0.07*			0.62	*0.14*	0.40	*0.22*
95	C33:1	0.09	*0.06*			0.11	*0.11*			0.01	*0.01*		
96	C33	0.07	*0.04*	0.03	*0.03*	0.54	*0.12*	1.29	*0.80*				
97	15+17C33:1									0.39	*0.17*	0.26	*0.26*
98	9+11+13+15+17C33	1.08	*0.09*	0.35	*0.35*	6.12	*0.61*	4.48	*1.13*	1.52	*0.35*	2.67	*0.60*
99	11,15+13,15+13,17C33	0.63	*0.25*	0.03	*0.03*	**6.30**	*1.32*	**9.46**	*3.01*	0.93	*0.18*	3.38	*0.68*
100	13,x+15,xC33	0.60	*0.39*										
101	7,11+7,15C33					0.67	*0.67*						
102	3C33									0.06	*0.02*		
103	5,xC33					0.89	*0.89*						
104	C34	0.03	*0.02*			1.02	*0.17*	2.21	*0.59*				
105	11+12+13+14+15+17C34	0.03	*0.02*			1.23	*0.16*	0.96	*0.23*				
106	C35:1									0.22	*0.10*		
107	15C35:1												
108	13,17+15,17C34												
109	3+4+5C34												
110	15C35:1									0.04	*0.02*	0.03	*0.04*
111	C35:1	0.02	*0.02*			0.11	*0.11*			0.14	*0.03*		
112	C35					1.80	*0.46*	1.20	*0.33*				
113	9+11+13+15+17C35	0.18	*0.06*	0.00	*0.00*	3.18	*0.93*	3.28	*0.27*	0.33	*0.11*	2.11	*0.38*
114	11,15+13,15+15,17+17,19C35	0.17	*0.07*	0.56	*0.56*	1.56	*0.65*			0.48	*0.22*	2.07	*1.00*
115	11,xC35												
116	7,11C35					0.10	*0.10*			0.01	*0.01*	2.70	*1.26*
117	C36												
118	11+12+13+14C36					0.29	*0.07*						
119	8C36												
120	C37:1					0.34	*0.15*						
121	C37					0.30	*0.12*	0.13	*0.04*				
122	13+15+17C37					0.77	*0.16*	1.66	*0.43*	0.23	*0.11*	0.22	*0.19*
123	11,x+13,x+15,xC37									0.11	*0.03*	0.99	*0.86*
124	C38												
125	Di MeC39												
	Total n-alKanes	27.94	*2.83*	28.68	*2.33*	20.39	*2.11*	17.86	*5.61*	8.68	*1.50*	25.38	*5.48*
	Total alkenes	0.27	*0.07*	0.00	*0.00*	2.14	*0.39*	0.15	*0.10*	3.33	*0.64*	0.51	*0.20*
	Total methyl-alkanes	71.79		71.32		77.47		81.98		87.99		74.11	
	n=	6		3		6		3		11		4	
	In bold % > 5%, in red alkenes in F se												

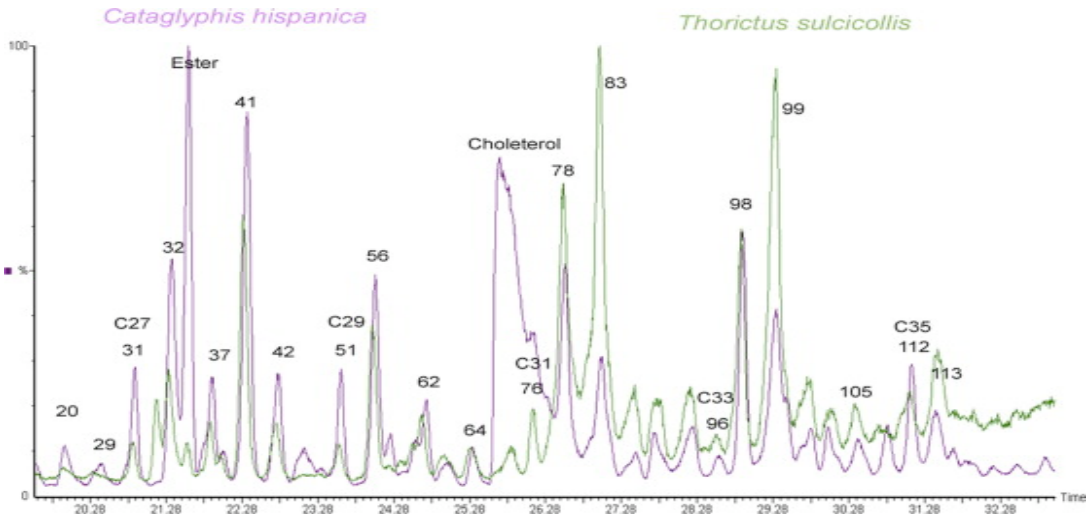

Figure S1 - Gas chromatograms of the CHCs of *Cataglyphis hispanica* and *Thorictus sulcicollis* . Peak numbers refer to the hydrocarbons described in Table S1.

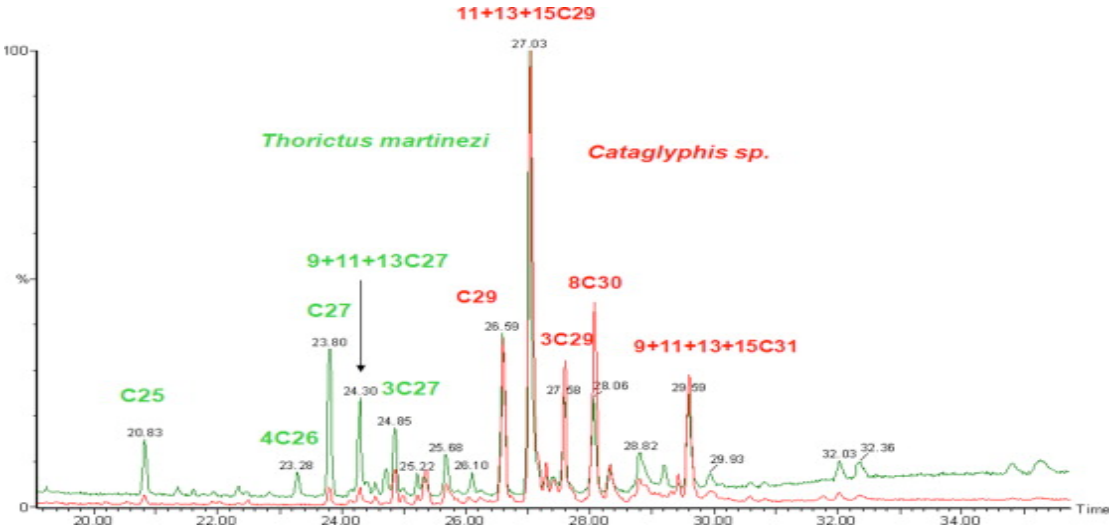

Figure S2 - Gas chromatograms of the CHCs of *Cataglyphis* sp and *Thorictus martinezi* . Peak numbers refer to the hydrocarbons described in Table S1.

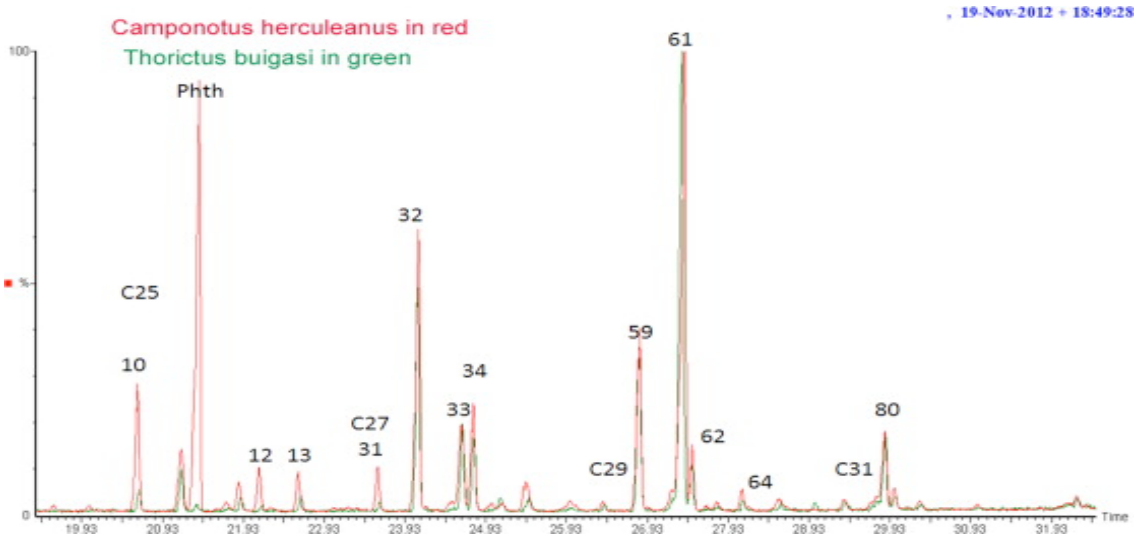

Figure S3 - Gas chromatograms of the CHCs of *Camponotus herculeanus* and adopted *Thorictus buigasi* . Peak numbers refer to the hydrocarbons described in Table S1.

Photo 1 - *Thorictus buigasi* in a *Formica selysi* colony.

Photo 2 - *Thorictus buigasi* in a *Camponotus herculeanus* colony.