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Co-evolution-driven cuticular hydrocarbon variation between the slave-making ant *Rossomyrmex minuchae* and its host *Proformica longiseta* (Hymenoptera: Formicidae)

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Summary. *Proformica longiseta* exists as two populations in the Sierra Nevada Mountains in Spain, only one of which is parasitized by the slave-maker ant *Rossomyrmex minuchae*. To investigate the possible effect of co-evolutionary pressures on cuticular hydrocarbon (CHC) profiles (the presumed nestmate recognition cues), we performed a comparative analysis of the CHC of *R. minuchae* and *P. longiseta* colonies from both the allopatric and sympatric populations; the latter includes samples of enslaved as well as free-living workers. Discriminant analyses based on these chemical profiles showed two clear profile groups: the first comprised *R. minuchae* and both enslaved and free-living *P. longiseta* from the sympatric population; and the second the allopatric *P. longiseta* workers. As expected, the profiles of the two sympatric *P. longiseta* groups (enslaved and free-living) were distinct; but, interestingly, those of the enslaved *P. longiseta* and its parasite *R. minuchae* were also distinguishable. This indicates that despite their cohabitation each species maintains its own chemical identity. Profile similarity between the sympatric free-living *P. longiseta* and its parasite may explain the lower than expected aggression observed during raids. We further speculate that in view of the differences between the sympatric and allopatric population of *P. longiseta,* co-evolutionary pressures have driven changes in the profile of the former to better match that of its parasite *R. minuchae*. Such an adjustment may have enabled nests of the sympatric *P. longiseta* to endure multiple raids by the parasite (due to the reduced aggression) and thus to continue to reproduce despite the damage inflicted by the raids.

Key words. Social parasitism – cuticular hydrocarbons – coevolution – *Rossomyrmex minuchae* – *Proformica longiseta*

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Introduction

Nestmate recognition is a key element in social insect organisation, enabling the exclusion of unrelated individuals and, in this way, preventing robbery, predation, competitors and social parasitism (Wilson 1971). Social parasites have consequently evolved means to bypass the recognition system in order to successfully usurp their host's nests. In obligatory parasites, such as slave-making ants, newly-mated females are not able to found a new colony independently, but must usurp a host nest and eliminate and replace the host queen(s) (Buschinger 1986; Hölldobler & Wilson 1990). In the parasitized nest the host workers care for the slave-maker brood and perform all other nest duties, while the slave-making workers specialize in raiding new host nests to supplement the depleted slave-worker force.

During usurpation, raids and cohabitation, such social parasites are able to exploit their host's communication code and thus achieve social integration and avoid aggression. Although the strategies employed by different parasite species are diverse, breaking the slave's nestmate recognition system is at the core of each of them. The ant recognition system is largely based on chemical cues, which are shared by all nest members and create a common colony odour, the "Gestalt odour" (Crozier & Dix 1979).

Among the strategies employed by parasites to integrate into their host colony is the existence and/or acquisition of similar chemical profiles between the social parasites and their hosts (see Lenoir *et al*. 2001). For example, chemical congruency is the basis of a peaceful coexistence of the shampoo ants of the genus *Formicoxenus* that live in association with their *Myrmica* hosts (Lenoir *et al*. 1997), as well as between *Harpagoxenus sublaevis* and its *Leptothorax* hosts (Kaib *et al*. 1993). Similarly, the cuckoo ant, *Leptothorax kutteri*, acquires the recognition labels of colonies of its host species, *L. acervorum* (Franks *et al*. 1990). In the genus *Polyergus* as well, the slave-making workers are able to adjust their cuticular hydrocarbon profiles to match that of the slave species (Yamaoka 1990;

D'Ettorre *et al*. 2002). This is in contrast to a previous study that reported that the cuticular profile of *P. rufescens* did not closely match that of its host (Bonavita-Cougourdan *et al*. 1996). Recently Brandt *et al*. (2005) described a chemical resemblance between *Protomognathus americanus* and its three closely related *Temnothorax* hosts, but they did not discuss whether this fine-tuned cuticular-profile adjustment is due to chemical mimicry or simply reflects chemical congruence. Finally, the mechanisms involved may be more complex, as exemplified by *P. americanus,* the workers of which chemically mark their slaves to prevent them from returning to their parental colony (Alloway & Keough 1990).

The interrelationship between the slave-maker ant *Rossomyrmex minuche* and its host *Proformica longiseta*, in particular the occurrence of parasitized and non-parasitized host populations (Ruano & Tinaut 1999; Zamora-Muñoz *et al.* 2003), provides a unique opportunity to investigate some of the mechanisms that enable the host population to endure usurpation and multiple raids by the slave-maker ant. Accordingly, we compared the variation in cuticular hydrocarbon (CHC) between the allopatric (parasite-free population) and the sympatric (parasite-prone population) host *P. longiseta* as well as that of the parasite *R. minuchae*, focusing on geographic distribution and on host-parasite relations.

Materials and methods

Collection and rearing of ants

Rossomyrmex minuchae and *Proformica longiseta* are endemic species to the Sierra Nevada Mountains in southern Spain; the former is also a protected species. Colonies of *R. minuchae* and *P. longiseta* were collected at two sites in the Sierra Nevada Mountains, Granada, Spain. In the first site - Dornajo (2000 m.a.s.l), both species are sympatric and the samples (collected in May 1996) included two enslaved colonies (mixed-species of *R. minuchae* and *P. longiseta*) (colonies 1, 2) and two free-living queenright colonies of *P. longiseta* (colonies 3, 4). These are considered as sympatric nests. In the second site - Borreguiles (2700 m.a.s.l), where *R. minuchae* is not present, we collected concurrently two free-living queenright *P. longiseta* nests (colonies 5, 6). These are considered as allopatric nests. Samples for chemical analyses were taken from each colony immediately after collection.

Chemical analyses

Identification of the cuticular hydrocarbons was accomplished using pools of at least 20 workers of *R. minuchae* from colony 7 and at least 20 workers of *P. longiseta* from free-living queenright colony 8 (both of Dornajo site). Analyses were done by gas chromatography/mass spectrometry (VGM250Q) at the EI mode (70eV, injector temperature 220 °C) using a DB-5 fused silica capillary column (Temperature program: 60 °C -280 °C at 10 °C /min; held at 280 °C for 30 min and then heated to 295 °C at 20 °C /min). The eluting CHC were identified by their fragmentation patterns and in comparison to synthetic series of alkanes ranging from eisosane to pentatriacontane.

Quantification and characterization of cuticular hydrocarbon profiles of *R. minuchae* and *P. longiseta* were conducted by gas chromatography, using total body washes. Individual ants were killed by freezing and then immersed in 1 ml of pentane for 10 min, after which the pentane was withdrawn to a new vial and evaporated to dryness. Extracts were re-dissolved in 50 µl of pentane containing pentadecane (*n* C_{15}) as internal standard, of which 1 µl was injected into an on-column Varian 3300 GC equipped with a capillary column (Chrompack CPSil 5 WCOT, 25 m, 0.25 mm Internal Diameter). The carrying gas was helium at 1 bar, and the temperature was programmed from 80 °C to 150 °C at 10 °C per minute and from 150 °C to 280 °C at 5 °C per min. Quantification was done by peak integration compared to the internal standard. For the statistical analyses, the relative percentage for each peak was calculated from the total of the peaks considered. Only identified peaks were used for profile characterisation. Similarity (or divergence) between the chemical profiles of individual ants was compared by discriminant analysis (Statistica for Windows ©) according to species and geographic distribution. For these analyses, we used two *R. minuchae / P. longiseta* mixed-species nests, and four free-living queenright *P. longiseta* nests (two sympatric and two allopatric). Statistical analyses were performed on 67 extracts (20 *R. minuchae* and 16 *P. longiseta* from mixed-species colonies 1, 2; 18 *P. longiseta* from sympatric free-living queenright colonies 3, 4; 13 P. *longiseta* from allopatric free-living queenright colonies 5, 6).

Results

Workers of *R. minuchae* and *P. longiseta* show qualitative similarity in cuticular hydrocarbon profiles consisting of 23 peaks and 32 identified hydrocarbons (Figure 1, Table 1), including a series of odd *n*-alkanes (C_{23}, C_{25}, C_{27} and C_{29}), monomethylalkanes and dimethylalkanes. The major peaks for *R. minuchae* were nonacosane (peak 11), 3-methylnonacosane (peak 13), a mixture of 8- and 10-methyltriacontane (peak 14), 8,14-dimethyltriacontane (peak 15), a mixture of 9- and 11-methylhentriacontane (peak 18), 9,17-dimethylhentriacontane (peak 19), and 8,14-dimethyldotriacontane (peak 22). The profile of *P. longiseta* contained the same major peaks, with the exception of nonacosane, which was found only in moderate amounts. There were some differences in the profile of *P. longiseta* between the two populations collected. Ants from sympatric nests possessed several branched hydrocarbons that were only present as traces in allopatric *P. longiseta* (for example, 3-methylnonacosane; 8- and 10-methyltriacontane, 8,14-dimethyltriacontane; 9- and 11-methylhentriacontane, 9,17-dimethylhentriacontane).

Figure 2 presents a discriminant analysis based on the chemical profiles of *R. minuchae*, enslaved and free-living sympatric *P. longiseta* as well as allopatric *P. longiseta*.

A plot of the first (82.8 % of the variance) and second variables (12.4 % of the variance) showed that individuals clustered together, forming four separate groups (90 % well clustered) ($F_{57,114} = 4.55$, $P<10^{-4}$). The first discriminant variable separated the free-living allopatric *P. longiseta* from all other groups ($F_{19, 38} = 15.96$, $P <10^{-4}$; $F_{19, 38} = 11.93$, $P < 10^{-4}$, $F_{19, 38} = 8.06$, $P < 10^{-4}$, respectively; Kruskal-Wallis test: H=153.45, $P <10^{-4}$). The second discriminant variable separated *R. minuchae* workers from the enslaved or free-living sympatric *P. longiseta* workers ($F_{19, 38} = 2.68$, $P = 0.0026$; $F_{19, 38} = 2.08$, $P = 0.028$, respectively). The enslaved *P. longiseta* were also separated albeit not significantly, from their sympatric free-living congeneric workers ($F_{19, 38} = 2.25$, $P = 0.065$).

A more detailed analysis using the Mahalanobis Distances (MD) between individuals in one group and the centroïds of other groups is presented in Figure 3. Within the groups of *R. minuchae* and the sympatric *P. longiseta* the distances between individuals and the centroïds of the other groups were not significantly different from that of intra-group (the distance between individuals and their own group centroïds). On the other hand all the inter-group distances

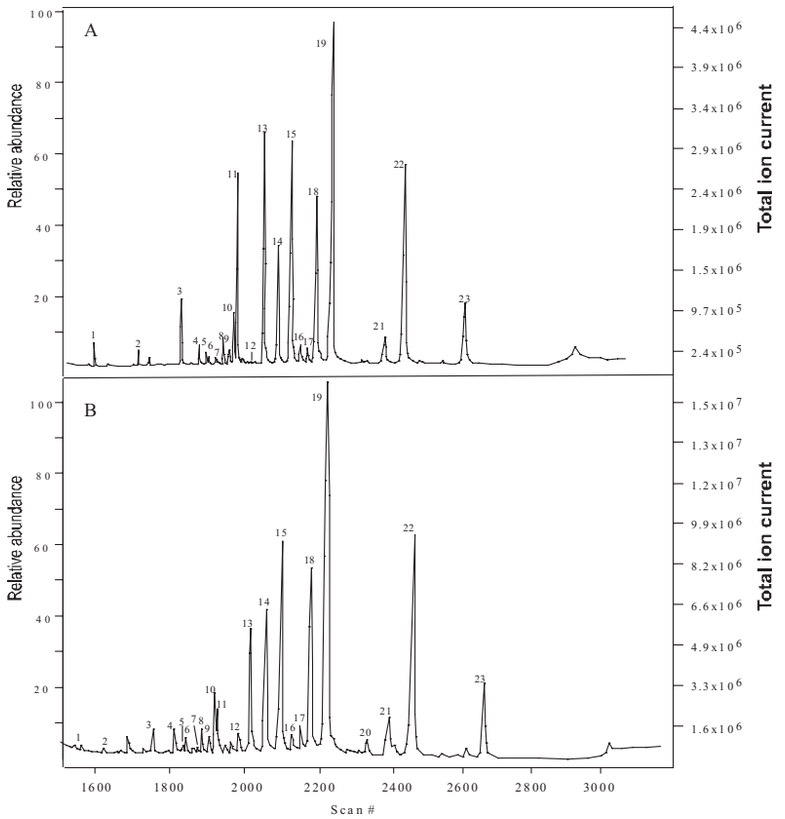

Fig. 1 Gas chromatograms (GS-MS) of total body washes of 20-pooled workers of *R. minuchae* (A) and free-living *P. longiseta* (B) collected from Dornajo site (colonies 7 and 8 respectively). Peak identifications: 1: C_{23}; 2: C_{25}; 3: C_{27}; 4: 3-MeC_{27}; 5: C_{28}; 6: 8–+10-MeC_{28}; 7: 6-MeC_{28}; 8: 4–MeC_{28}; 9: 6,10+6,14-DiMeC_{28}; 10: 4, 8+4,10-DiMeC_{28}; 11: C_{29}; 12: 5-MeC_{29}; 13: 3-MeC_{29}; 14: 8–+ 10-MeC_{30}; 15: 8,14-DiMeC_{30}; 16: 4-MeC_{30}; 17: 6,14-Di-MeC_{30}; 18: 9–+11-MeC_{31}; 19: 9,17-DiMeC_{31}; 20: 5,17-DiMeC_{31}; 21: 8–+10-MeC_{32}; 22: 8,14-DiMeC_{32}; 23: 9,17-DiMeC_{33}

Table 1. Comparative chemical analyses (from GC-MS) of the major cuticular hydrocarbons of free-living (allopatric and sympatric) and enslaved *P. longiseta* workers and of the slave-maker *R. minuchae* workers. T Indicates trace amounts.

		P. longiseta			***R. minuchae***
		Free living		Enslaved	Slave-maker
Peak	Compound	*Allopatric*	*Sympatric*		
1	C_{23}	0.01 ± 0.01	0.59 ± 0.30	0.27 ± 0.08	0.92 ± 0.29
2	C_{25}	0.02 ± 0.02	1.07 ± 0.51	0.50 ± 0.17	0.95 ± 0.31
3	C_{27}	5.79 ± 0.93	2.45 ± 0.45	1.87 ± 0.59	2.22 ± 0.50
4	3 Me C_{27}	0.89 ± 0.15	0.61 ± 0.12	1.87 ± 1.30	1.11 ± 0.56
5	C_{28}	1.16 ± 0.19	0.68 ± 0.15	0.54 ± 0.20	0.79 ± 0.19
6	8 +10 Me C_{28}	3.67 ± 1.19	1.43 ± 0.35	0.43 ± 0.12	0.79 ± 0.15
7	6 Me C_{28}	T	0.80 ± 0.21	1.40 ± 0.56	1.19 ± 0.60
8	4 Me C_{28}	0.70 ± 0.17	0.83 ± 0.30	0.12 ± 0.09	0.57 ± 0.30
9	6,10 DiMe C_{28} (+ 6,14 DiMe)	0.30 ± 0.13	0.66 ± 0.11	0.61 ± 0.61	0.94 ± 0.13
10	4,8 + 4,10 DiMe C_{28}	8.29 ± 1.01	5.01 ± 1.15	0.69 ± 0.32	2.82 ± 0.66
11	C_{29}	12.00 ± 0.86	4.65 ± 1.10	2.60 ± 0.71	6.41 ± 1.64
12	5 Me C_{29}	7.37 ± 0.93	0.89 ± 0.37	0.40 ± 0.23	1.75 ± 0.43
13	3 Me C_{29}	0.98 ± 0.74	4.02 ± 0.94	4.08 ± 1.12	4.21 ± 0.95
14	8 +10 Me C_{30}	T	4.54 ± 0.92	2.45 ± 0.95	7.49 ± 1.78
15	8,14 DiMe C_{30}	0.30 ± 0.13	7.21 ± 1.57	4.30 ± 1.73	6.41 ± 2.29
16	4 Me C_{30}	11.55 ± 1.15	0.81 ± 0.38	0.40 ± 0.24	0.83 ± 0.59
17	6,14 DiMe C_{30}	0.14 ± 0.14	1.84 ± 1.30	0.17 ± 0.10	0.90 ± 0.20
18	9 +11 Me C_{31} (+15 Me)	T	3.10 ± 1.41	0.05 ± 0.05	3.12 ± 2.06
19	9,17 DiMe C_{31}	T	8.50 ± 1.69	1.38 ± 0.31	9.17 ± 2.15
20	5,17 DiMe C_{31}	T	0.08 ± 0.05	0.84 ± 0.32	0.48 ± 0.11
21	8 +10 Me C_{32}	14.73 ± 2.33	1.22 ± 0.31	0.12 ± 0.12	0.19 ± 0.18
22	8,14 or 8,16 DiMe C_{32}	T	2.42 ± 0.47	0.89 ± 0.41	4.21 ± 1.56
23	9,17 + (9,15+9,19) DiMe C_{33}	T	0.75 ± 0.31	0.83 ± 0.28	0.13 ± 0.04

Me and DiMe correspond to methyl and dimethyl respectively. Values indicate, for each compound, the mean relative percentage (± SEM) for a 10 min extraction with pentane. Values are calculated for free living *P. longiseta* workers (Allopatric $N = 13$, Sympatric $N = 18$), Enslaved *P. longiseta* workers ($N = 16$), slave-maker *R. minuchae* workers ($N = 20$).

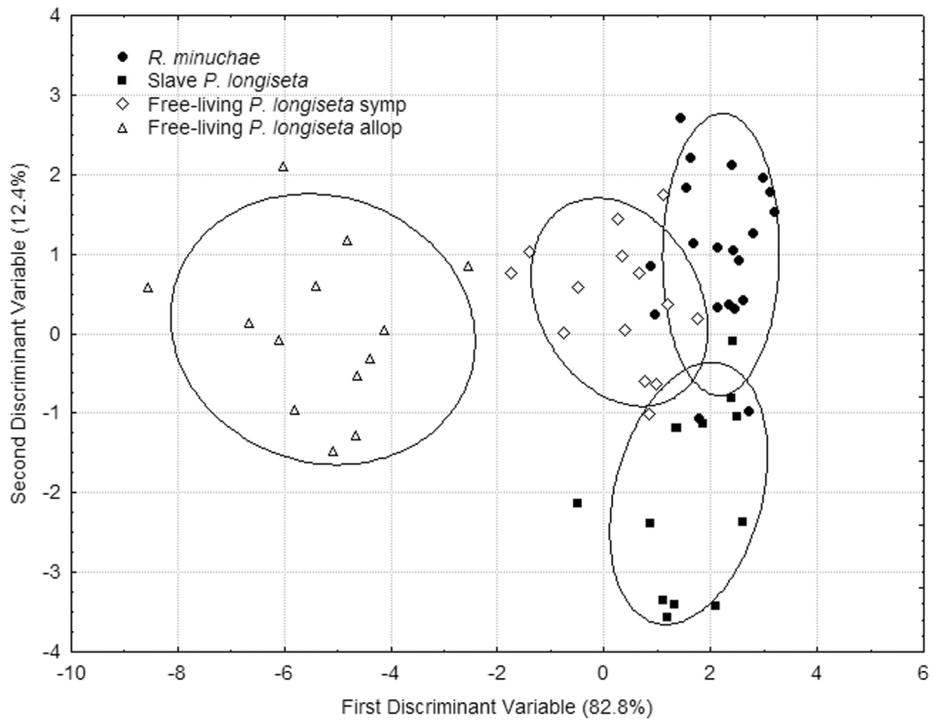

Fig. 2 Discriminant analysis (Ward's method, Euclidean distances) conducted on the relative proportions of the 23 peaks of the cuticular profiles of *R. minuchae* and *P. longiseta* workers from the two mixed colonies (nine *R. minuchae* and four *P. longiseta* from mixed-species colony 1, eleven *R. minuchae* and twelve *P. longiseta* from mixed-species colony 2), sympatric free-living queenright *P. longiseta* from Dornajo (ten *P. longiseta* from colony 3 and eight from colony 4), allopatric free-living queenright *P. longiseta* from Borreguiles (six *P. longiseta* from colony 5 and seven from colony 6)

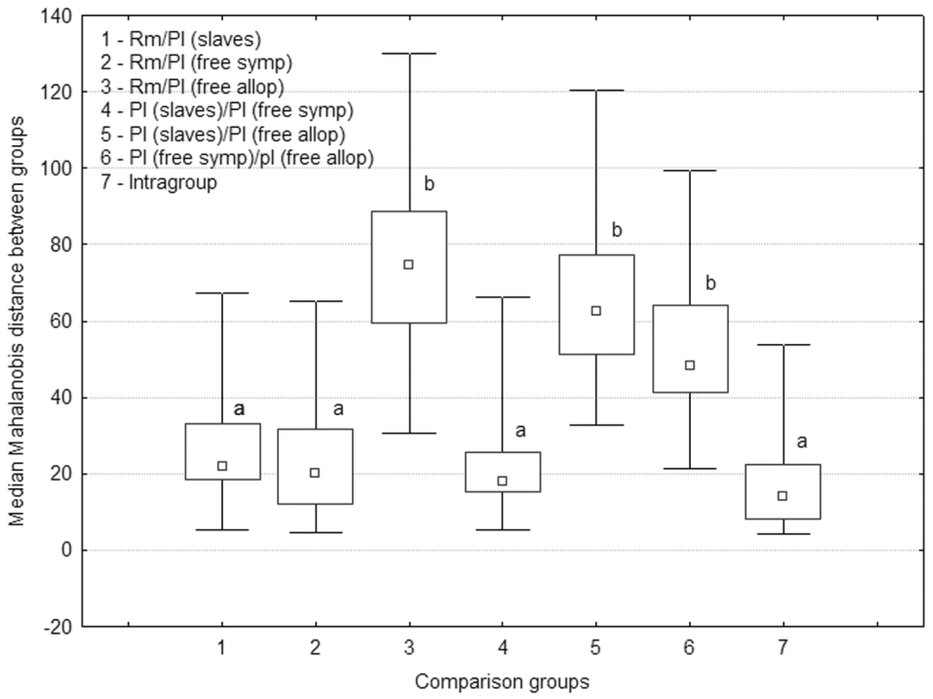

Fig. 3 Median Mahalanobis distance between groups. Different letters represent the groups, which differed significantly (Kruskal-Wallis test, $P < 0.001$, N = 256). Intragroup distances are averaged for all groups

concerning individuals from the allopatric population were significantly higher than the intra-group (Figure 3, Kruskal-Wallis test: $P < 10^{-4}$). Such low inter-group variation within the sympatric *P. longiseta* and the parasite may result in the misclassification of individual ants to another group, which is consistent with the hypothesis that selection for low aggression during raids has resulted in profile congruency between the parasite and its host.

Discussion

Although there was qualitative resemblance between the CHC profiles of *R. minuchae* and *P. longiseta*, examination of multiple profiles revealed qualitative differences that were sufficient for discriminating between the two species. Greater quantitative differences were found between the two distinct populations of *P. longiseta* sampled (sympatric parasite-prone and allopatric parasite-free populations). These differences were expressed mainly in the branched alkanes, which is consistent with their presumed role in nestmate recognition (Bonavita-Cogourdan *et al.* 1987; Provost 1992; Gamboa *et al*. 1996; Astruc *et al*. 2001; Errard *et al*. 2006). Most important is that the profiles of *R. minuchae* were more similar to those of the sympatric free-living *P. longiseta* rather than the allopatric population.

It is noteworthy that even when enslaved, individual *P. longiseta* continued to maintain a distinct cuticular signature that, although not significantly so, was closer to that of free-living individuals than to the slave-makers. Two features can explain how the slave and the parasite coinhabit the same nest despite having seemingly disparate cuticular profiles. First, it is possible that such quantitative dissimilarities are not large enough to elicit aggression since both the slave-maker and the slave share the same hydrocarbons. Second, since the slaves actually eclose in the slave-maker's nest, they imprint on the parasite's odour and become its worker force (Errard 1994; Schumann & Buschinger 1995). It is probable that the slave-maker odour was incorporated into the slave template, resulting in recognition of the slave-maker as nestmates (Errard *et al*. 2006). Host-parasite profile disparity also indicates that there is no or little odour exchange between the two species. A similar pattern was also shown in mixed-species groups of *Manica rubida* and *Myrmica rubra*, in which heterospecific workers hardly exchanged hydrocarbons (Vienne *et al.* 1995; Errard *et al*. 2006).

There is evidence for chemical mimicry as a social integration strategy in several social parasites, such as the slave-making ants *Polyergus* (D'Ettorre *et al*. 2002). For example, the Japanese species *P. samurai* shows the same cuticular hydrocarbon pattern as the host present in the colony (*Formica japonica* or *F. hayashi*) (Yamaoka 1990). Chemical similarity was also found in established colonies of *P. breviceps* and the *Formica* hosts (Howard & Akre 1995).

We suggest that the profile similarity exhibited between the slave-maker and its sympatric, but not allopatric host, is an adaptation enabling the host nest to sustain raids by their parasite, and thus favourably selected. Due to habitat limitation (in particular for the slave-maker) the host nests that live in sympatry are constantly subjected to multiple raids by *R. minuchae* workers. This is consistent with field observations that revealed that during raids aggression between the raiding workers and the raided host is lower than expected (Ruano & Tinaut 1999, 2004). Convergence of the recognition cues may be one reason why heterospecific encounters do not culminate in an "all out war". It is not clear whether the profile of *R. minuchae* converged to that of its host as an adaptation that reduces the raided worker's resistance, or whether the profile of *P. longiseta* converged to that of the slave-maker to reduce the aggression of the latter. The restrictive distribution of *R. minuchae* to about 2000 m.a.s.l in the mountains of the Sierra Nevada in Spain may have imposed constraints on the species with respect to host selection, resulting in profile convergence to specific host population. However, we tend to exclude this possibility in favour of the hypothesis that it was the profile of *P. longiseta* that converged to that of *R. minuchae.* Two facts support the latter hypothesis. If *R. minuchae* was the species that changed we would have expected similarity between the two *P. longiseta* populations (since there was no selection on either population to change) rather than the observed disparity, which is an indication that the sympatric population shifted towards its slave-maker profile. This is also consistent with the fact that *P. longiseta* is rather docile while *R. minuchae* is quite aggressive. It is a common characteristic of slave-making ants to produce workers specialized for fighting, which regularly conduct slave raids on neighbouring host colonies and steal their brood to replenish the labour force (D'Ettorre & Heinze 2001). Above all it is clear that aggressive raids are much more detrimental to *P. longiseta* than to *R. minuchae* and any means to reduce this aggression enables the former species to endure multiple raids yet retain sufficient resources to reproduce in the following season (Zamora-Muñoz *et al*. 2003). Thus chemical congruency between the slave-maker and its free-living host is adaptive to both partners and therefore favourably selected.

Chemical convergence also explains the interesting finding that the enslaved ants maintain their own CHC profile. Both the initial odour similarity that presumably reduces aggression during raids and the olfactory imprinting at emergence of the slave, should reduce intra-nest aggression between the two species to minimum or none, thus making selection for odour homogenization unnecessary.

The present study exemplifies the plethora of mechanisms used by parasites to invade the host nest, and the counter-measures used by the potential host to minimize if not eliminate the parasite success. These include the modulation of host aggression to match the raiding season, as reported for the slave-maker *Protomognathus americanus* and its host *Temnothorax* (Brandt *et al*. 2005) and for the slave-maker *Polyergus rufescens* and its host *Formica rufibarbis* (D'Ettorre *et al*. 2004). Seasonal shifts in the acceptance threshold of the host to match the raiding season (Brandt *et al*. 2005; D'Ettorre *et al*. 2004), presumably reduce the costs of defence and/or change the outcome of raids. By revealing the chemical mechanism that enables the host population to sustain usurpation and multiple raids by the slave-maker ant, we address a fundamental problem in evolutionary biology: i.e. the evolutionary process by which parasites break into their host defence and the modulation of such defences to minimize parasite damage. The data presented here suggest that chemical coevolution of the CHC profile of the host *P. longiseta* (Zamora-Muñoz *et al*. 2003) is the basis for the observed phenomena (Brandt *et al.* 2005).

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