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CHEMICAL ECOLOGY AND SOCIAL PARASITISM IN ANTS

A. Lenoir, P. D'Ettorre, and C. Errard
[1]*Institut de Recherche sur la Biologie de l'Insecte—UPRES A 6035 Centre National de la Recherche Scientifique, Faculté des Sciences, F-37200 Tours, France; e-mail: lenoir@univ-tours.fr, dettorre@univ-tours.fr, errard@univ-tours.fr*

A. Hefetz
[2]*Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Ramat Aviv 69978, Israel; e-mail: hefetz@post.tau.ac.il*

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■ **Abstract** The chemical strategies by which parasites manage to break into the social fortresses of ants offer a fascinating theme in chemical ecology. Semiochemicals used for interindividual nestmate recognition are also involved in the mechanisms of tolerance and association between the species, and social parasites exploit these mechanisms. The obligate parasites are odorless ("chemical insignificance") at the time of usurpation, like all other callow ants, and this "invisibility" enables their entry into the host colony. By chemical mimicry (sensu lato), they later integrate the gestalt odor of this colony ("chemical integration"). We hypothesize that host and parasite are likely to be related chemically, thereby facilitating the necessary mimicry to permit bypassing the colony odor barrier. We also review the plethora of chemical weapons used by social parasites (propaganda, appeasement, and/or repellent substances), particularly during the usurpation period, when the young mated parasite queen synthesizes these chemicals before usurpation and ceases such biosynthesis afterwards. We discuss evolutionary trends that may have led to social parasitism, focusing on the question of whether slave-making ants and their host species are expected to engage in a coevolutionary arms race.

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INTRODUCTION

The natural history of parasitism is a fascinating question for evolutionary biologists, for whom the origins of social parasites among social insects are main topics. Because colonies of most social insects are closed to aliens, the means by which a parasite knocks on the colony's door and enters has provided an intriguing evolutionary problem to Schmid-Hempel (101). Wilson (129), Buschinger (25), Hölldobler & Wilson (70), and Tinaut & Ruano (114) have defined the various forms of associations among ant species according to a progressive increase in the degree of interaction, from cohabitation without direct contact between the species to complete integration of the parasite within the host colony. Plesiobiosis refers to two species sharing the same microhabitat without any further interactions. In cleptobiosis and lestobiosis (also called kleptoparasitism in other animals), an association exists, but the interactants occupy separate nests: cleptobiotic ants feed in their host's kitchen middens or rob food during trophallaxis between host workers, whereas the thief (lestobiotic) ants steal brood from neighboring ant colonies of another species. Parabiosis is a mutualistic relationship between two or more species that share the same nest but keep chambers and broods separate and do not interact directly. Xenobiosis refers to a more integrated association, in which the xenobiotic species lives and forages inside the host colony but keeps its brood apart. Xenobiotic species cannot live independently of the host. More integrated social parasites depend on labor provided by the host species workers. Such parasites include species whose colony-founding queens invade the nests of other species, may or may not kill the host queen, and use the workers as laborers. If they kill the host queen, two categories are recognized: temporary social parasites and slave-making ants. In the first association, the parasites progressively produce their own workers, which replace the host workers. The colony thus slowly develops from a mixed parasite-host colony to a pure society that does not need the host. The second category comprises slave-making ants (also called dulotic ants) that have to continually raid other ant nests for worker brood to refresh the labor force. Inquilinism is a permanent parasite-host association without slave raiding. In its more extreme expression, the invading queen produces sexual offspring only, allowing the host queen to survive and furnish a continuous supply of workers. The latter is the ultimate, degenerate stage of parasitism. Parasitism is not frequent, typifying only $\sim$220 described ant species of the more than 10,000 that are known. Parasites are not equally spread among the ant subfamilies; they are absent in the primitive subfamily Ponerinae, and in the Myrmicinae and Formicinae they are concentrated in certain genera (70).

We review the chemical strategies by which parasites manage to break into the social fortresses of ant colonies. We show that semiochemicals used for interindividual nestmate recognition are also involved in the mechanisms of tolerance and association between the species. We compare these strategies when appropriate with those used by other social insects, for example, wasps. We also review the plethora of chemical weapons used by social parasites. Finally, we discuss evolutionary trends that may have led to social parasitism, focusing on the question of whether slave-making ants and their host species are expected to engage in a coevolutionary arms race.

THE "GESTALT MODEL" FOR NESTMATE RECOGNITION

Social insects have evolved a highly developed recognition system enabling them to behave altruistically towards nestmates but reject alien conspecifics. The discrimination is based on chemical cues (or labels) that form a visa—the "colony odor." These cues are used by one individual to classify other individuals by comparison to its own representation or template. The template is defined as an internal representation of the labels expected in other individuals (see 34, 79). Hydrocarbons (HCs) from the cuticle are now considered to be the main chemical cues responsible for nestmate recognition in ants and wasps (84, 88, 104), although their role is still debatable (60, 102, 121). Direct experimental evidence that cuticular HCs, but not other cuticular lipids, are responsible for nestmate recognition was recently presented for *Cataglyphis niger* (80). These HCs are mainly linear and branched alkanes (chain length between C_{23} and C_{32}) of low volatility, which are sometimes accompanied by alkenes and alkadienes. Within the colony, the individuals share their recognition cues to form a common odor blend, according to the "gestalt model" of Crozier (32) and Crozier & Dix (33). This model has been behaviorally demonstrated in many species (see 84, 121), and chemical studies by Soroker et al (109), using radioactive compounds, have confirmed that individual ants acquire a common, uniform colony odor according to the gestalt model in *C. niger*. New data have recently been presented on *Camponotus fellah* and *Aphaenogaster senilis*, confirming the gestalt odor (A Lenoir, V Soroker, T Simon, A Hefetz, submitted for publication). Studies have also demonstrated that HCs are stored in the post-pharyngeal gland (PPG) and exchanged between members of the colony by trophallaxis, allogrooming, and physical contact (108; A Lenoir, V Soroker, T Simon, A Hefetz, submitted for publication). Despite its uniformity, the colony odor is dynamic and may change spontaneously over time or according to season, as reflected in quantitative changes in the relative proportions of the different cuticular HCs (21, 38, 86, 93, 98, 122; A Lenoir, D Cuisset, A Hefetz, submitted for publication). Alternatively to the gestalt model, Crozier & Dix (33) proposed the individualistic model for small colonies. In these cases, the individual labels are not mixed, and, when transfer does occur, it is at low levels and mediated by a few incidences of allogrooming and physical contact. For example, the ponerine *Pachycondyla apicalis* studied by Soroker et al (106) does not engage in trophallaxis and has a low level of allogrooming. Accordingly, the efficiency of HC transfer is very weak compared with that in the other formicine and myrmicine species. It was hypothesized that, in such species, colonial identity is based on individual odors and individual recognition (A Lenoir, D Cuisset, A Hefetz, submitted for publication). This model was already hypothesized by Crosland (31) on the basis of behavioral experiments in the ponerine *Rhytidoponera confusa*.

CHEMICAL INSIGNIFICANCE AND CHEMICAL INTEGRATION

Odor Changes with Age

Since the early work of Fielde (56), who hypothesized the existence of a progressive odor change with age in ants, many authors have confirmed this by behavioral observations in various ant species (see 84). A few studies have also shown an age-dependent quantitative variation in the production and release of the cues implied in formation of colonial odor. Newly eclosed ant workers are called callows. *Camponotus vagus* and *C. floridanus* callows have been shown to have a distinct cue profile that differs from that of adults (18, 91; see 121). In *Manica rubida* and *Formica selysi* workers, chemical analysis has shown that both species have low amounts of HCs (0.15 and 0.12 μg/mg of insect body weight, respectively) on the cuticle at 5 h postemergence, but 48 h thereafter, the amount rises to 0.3 and 0.22 μg, respectively, and each species demonstrates its own specific cuticular profile. Total HC amounts keep increasing with age until stabilization at the age of 1 month (0.6 μg for both species) (52; C Errard, unpublished data). In *C. niger*, callow ants have a small, rather undeveloped PPG, which develops structurally and chemically with age. The HC quantity in the gland increases accordingly from 1.2 μg per ant at emergence to 4 μg per ant in 1-day-old ants, 15.8 μg per ant after 7 days, and $\leq$28 μg per ant in mature ants (107). This progressive increase in HCs reflects a progressive increase in biosynthesis as was demonstrated, using radioisotopes, in virgin alate queens of *C. niger* (81). In *Cataglyphis iberica*, the worker PPG profiles are distinctive according to age group and gradually but slowly converge from a “callow profile” with specific HCs to a profile characteristic of mature workers. The quantities of HCs in this species increase from 0.06 to 0.08 μg/gland at emergence to 1.3 to 1.6 μg/gland in mature workers (37). A similar progressive increase in HC quantities on the cuticle and in the PPG of *A. senilis* and *Myrmicaria eumenoides* (133; A Lenoir, unpublished data). This chemical ontogeny corroborates nicely the studies pertaining to the ontogeny of nestmate recognition as shown below.

Cuticular Chemical Insignificance and Chemical Integration

Lenoir et al (84) termed the lack of external chemical substances of newborn ants "cuticular chemical insignificance." This short stage at the beginning of adult life is followed by a period of "chemical integration" when the callow ant synthesizes its own HCs and adsorbs chemicals from its nestmates or nest material to integrate into the colony gestalt. The weak signal that callow workers possess on their cuticle probably explains why they are more likely to be accepted into alien colonies than a 1-week-old worker, explaining the "acceptance period" of Stuart (113; see 27, 84 and chemical data in 94). The lack of colony specificity in HC composition of callow workers was also observed in other social Hymenoptera; newly emerged honeybees and wasps can be adopted in any conspecific colony (wasps *Ropalidia*: 9, *Polistes*: 104, bees: 58). In wasps, methyl-branched HCs, which are important in the colonial identity, are less frequent on the cuticle of newly emerged adults (89). During the chemical integration period, the mature ants recognize callows as such and exhibit specific behavior toward them. For example, in the polycalic ant *C. iberica*, young workers are transported by their older nestmates between the satellite nests (36). In *C. vagus*, callows experimentally deposited in the foraging arena are retrieved into the nest (19). The chemical-insignificance hypothesis may explain also intraspecific cleptobiosis, or food robbing between neighboring colonies of the same species, performed by particular *Ectatomma ruidum* thief workers that have reduced quantities of cuticular compounds (23, 77). These workers seemingly bear a callowlike odor and therefore could be partly chemically "invisible" and thus mistaken as nestmates. However, the chemical-insignificance hypothesis may not be the only explanation for the above behaviors toward callows. An alternative or complementary hypothesis is that newborn workers possess a secretion that attracts the adults and inhibits their aggression, as was suggested for *Formica* spp. (75), but chemical data supporting this hypothesis are still wanting. Callow workers of the slave-making ant *Polyergus rufescens* seem to possess a secretion that is very attractive for *Formica* host workers and can be acquired by anal trophallaxis, facilitating the adoption of the slave makers (43). Anal trophallaxis was also observed in queens and workers of another slave maker, *Protomognathus americanus*, but in this case the secretion does not seem to be attractive for hosts (111).

The chemical insignificance of callows follows a general phenomenon in insects in which HC biosynthesis ceases during the molt. For example, in *Blattella germanica*, it stops 2 days before the imaginal molt (131). In Lepidopteron larvae, HC biosynthesis is also interrupted during ecdysis, and because none of the HCs present on the old cuticle are reabsorbed before the molt, the larvae consequently lose all of their cuticular HCs during each molt (40, 45, 63). Hydrocarbon biosynthesis is resumed soon after the molt, and their quantities on the cuticle increase thereafter. In *Drosophila mojavensis*, the quantity of cuticular lipids doubles during the first 14 days of adult life, from 1.8 to 3.6 μg/fly (62). Low levels of cuticular lipids in young individuals were also reported for other terrestrial arthropods [e.g. the spiders (*Tegeneria*; 117)]. Although the molt presents a period of vulnerability because of desiccation risks, it seems to have evolved to be very important for socialization in social insects. The cuticle of callow individuals can adsorb a lot of substances (establishment of the chemical visa), and this is then followed by a learning period (establishment of the template).

Mixed Colonies

According to Foitzik & Heinze (57), intraspecific mixed colonies are frequent in *Leptothorax nylanderi*. After hibernation, a temporary overabundance of empty sites facilitates the fragmentation of larger colonies into small buds, which are in part queenless. In summer, on the other hand, a severe shortage of suitable nest sites leads to the fusion of unrelated colonies that, after initial fighting, permanently merge and cohabit. Typically, one queen survives after fusion. This temporary intraspecific slavery is widespread in the genus *Leptothorax* and may be an important step to obligatory permanent parasitism (57). How are non-nestmate workers able to cohabit in these colonies? *Leptothorax* spp. inhabit cavities in rotting branches, hollow acorns, and grass stems, and the colony odor is very flexible and influenced by the nest material (68, 112). This colony odor plasticity may facilitate the establishment of a common colony odor. Many other cases of raiding behavior leading to intraspecific slavery are known (70), but no chemical data are available.

The creation of artificial mixed-species groups provides an excellent tool for testing the chemical insignificance followed by the chemical integration modes of alien-ant adoption. In mixed-species groups composed of *F. selysi* and *M. rubida*, Bagnères et al (10) showed that the ants acquire some of the components characteristic of their allospecific nestmates. This acquisition is achieved by mutual exchange of the specific cues found in their PPGs, rather than the de novo synthesis of the allospecific HCs (126). The two species thus cohabit without aggression presumably because workers share the same mixed-species odor. Likewise, it was demonstrated that in mixed-species groups of termites, the cuticle adsorbs allospecific HCs to form the mixed-colony odor (123, 124). The fact that in these mixed groups the allospecific members are recognized as nestmates and are integrated as a homogenous group implies that the template they use is acquired through learning. In all of the ant species studied so far, the reference cues are learned shortly after the emergence (see 34, 48). Learning of social attachment also concerns the queen (6, 125), as well as constituting the basis of integration of host workers into the mixed colony by slave makers (see 76, 82, 103).

Although the use of artificial mixed-species groups provides an excellent tool for studying the involvement of chemical cues in allospecific interactions, it does not necessarily reflect a natural situation. We assume that naturally occurring mixed-species associations have a long coevolutionary history that may have shaped alternative mechanisms for colony integration. Nonetheless, some of the mechanisms that have been studied support chemical insignificance as a naturally occurring strategy for colony usurpation by parasites.

Parabiotic Associations

Only a few parabiotic associations in ants have been studied from a chemical point of view, two of which can serve as examples. Orivel et al (96) studied arboreal ant gardens in the tropical forests of the Americas, where two or three ant species can live in the same garden and share the same trails without aggression. In the studied pairs (*Crematogaster limata parabiotica-Camponotus femoratus* and *Pachycondyla goeldii-Odontomachus mayi*), the ants keep their own cuticle-specific profile. Ants are tolerant towards ants belonging to the allospecific colony with which they share the garden (nestmates), but not towards individuals from the same species that occupy different gardens (non-nestmates). Thus, despite the fact that their own HCs differ from those of the allospecific ants, the ants are able to discriminate between different allospecific colonies. The hypothesis is that within an association, the ants learn, through a familiarization period, the HC profiles of their associative species (96).

In Chile, *Camponotus chilensis* and *Camponotus morosus* are sometimes found in parabiosis with *Brachymyrmex giardii*. Although the above *Camponotus* species are very intolerant toward alien conspecific or allospecific ants, *B. giardii* appear to be more tolerant and readily associate with either of the above two *Camponotus* species. Behavioral experiments have demonstrated the ability of those ants that live in parabiotic nests to discriminate nestmate from non-nestmate individuals of the associated species. Analysis of the cuticular chemicals has shown that, in the association *C. morosus-B. giardii*, each species keeps its own specific cuticular profile. However, in the association *C. chilensis-B. giardii*, the workers of the two species acquire some of the allospecific cuticular components. These observations indicate that the tolerance of allospecific ants may in some cases be independent of congruency in chemical cues. In this situation, the allospecific profile must be learned (50; C Errard & J Ipinza Regla, unpublished data). However, we cannot exclude the possibility that there are other pheromonal cues that enable these associations, despite the differences in cuticular HCs.

Another example of parabiosis is provided by Espelie et al (54) for the acacia ants of Central America, *Pseudomyrmex ferrugineus*, which tolerate nests of the wasp *Parachartegus aztecus* on the same *Acacia* tree but drive away all other insects including ants. A chemical congruency found between the wax layer of the plant and the cuticular HCs of the ant and the wasp explains this tolerance and supports the hypothesis of a biochemical coevolution of the three species.

PROPAGANDA, APPEASEMENT, AND REPELLENT SUBSTANCES

Successful parasitism depends on successful invasion of the host nest, as well as the ability to remain in the host colony without being expelled or killed. These are major problems for parasites, which must “break into the fortress” of the host colony (101). Table 1, based on the work of Hölldobler & Wilson (70), presents

TABLE 1 Chemical weapons involved in social parasitism in ants

Major products	Chemical class	Role	Ant	Gland	Reference
6-methyl-5-hepten-2-one	Ketone	Alarm defense Mimetic of alarm pheromone of *Tapinoma*	*Bothriomyrmex syrius* alate females (not in workers)	Pygidial gland (anal gland)	87
2-butyl-5-heptylpyrrolidine	Alkaloid	Repellent during brood raiding	*Diplorhoptrum fugax* workers	Poison gland	15
n-heptadecene, n-heptadecadiene	Alkanes	Propaganda pheromone	*Harpagoxenus sublaevis* workers	Dufour's gland	95
Decyl, dodecyl, tetradecyl acetates (C_{10}, C_{12}, C_{14} acetates)	Esters	Propaganda: panic and dispersion of defenders' hosts during slave raids Alarm pheromone attracting the slave makers	*Formica subintegra* *F. pergandei* (*F. sanguinea* group)	Dufour's gland	99
Decyl, undecyl, dodecyl acetates (C_{10}, C_{11}, C_{12} acetates)	Esters	?	*F. sanguinea* queens and workers Mimetic of *F. fusca* and *F. rufibarbis* slaves	Dufour's gland	13
Undecane (n-C_{11})	Alkanes				
Farnesene	Terpenes		Farnesene only in old workers		3
Decyl butanoate[a]	Ester	Repellent Appeasement allomone	*Polyergus rufescens* queens during usurpation	Dufour's gland	44 127
Octadecyl butanoate	Ester	Repellent during raids?	*P. rufescens* workers		44
Tetradecanal (+ dodecyl aldehyde and heinecosene)		?	*Rossomyrmex minuchae* virgin queen	Dufour's gland[b]	
Heinecosene					
Tricosene			*R. minuchae* queen in host nest		
Tricosane (and complex mixture of alkanes)			*R. minuchae* worker		

[a] Misidentified as decyl isobutyrate in (127), errata in (105).

[b] A Hefetz, A Lenoir, F Ruano, A Tinaut, unpublished data.

all of the known cases in which parasites use offensive chemicals to disrupt their host's defense system. (For recent general references on pheromones in social insects, see 14, 120.)

In associations like cleptobiosis and lestobiosis, a simple technique is to use chemical weapons to disturb the targeted allospecific colony workers and use this time to steal the brood. Blum et al (15) showed that the thief ant *Diplorhoptrum fugax*, which steals brood from neighboring colonies, during a raid emits a powerful repellent from its poison gland, the secretion of which is fortified with *trans*-2-butyl-5-heptylpyrrolidine. This noxious chemical causes the nurse ants to abandon their brood, enabling the *D. fugax* workers to rob it. It is not known whether ants like *Cerapachys* spp., which also raid nests to obtain allospecific broods, use similar chemical strategies to invade the target colony.

Queens of the temporary social parasite *Bothriomyrmex syrius* studied by Lloyd et al (87) use both visual and olfactory cues to successfully invade their host *Tapinoma simrothi*. Unlike their light-brown workers, *B. syrius* queens are dark and look like their host queen. Moreover, the pygidial gland of the queen contains a ketone 6-methyl-5-hepten-2-one, like its *Tapinoma* host, but it lacks the *cis* 3-dodecenoic acid typical of workers of *Bothriomyrmex* spp. The ketone is an alarm pheromone and a defensive substance of the *Tapinoma* workers, and although the exact mechanism of invasion in this system is still obscure, it is assumed that this chemical mimesis assists the parasite to elude the host workers.

The use of offensive chemicals is the tactic used by the North American slave makers of the *Formica sanguinea* group (*Formica subintegra* and *Formica pergandei*) to invade their host, as has been studied by Regnier & Wilson (99). The Dufour's gland of the slave makers is hypertrophied and is the source of the pheromone bouquet composed of C_{10}, C_{12}, and C_{14} acetates, 2-tridecanone, and tridecane. The acetates play an important role during nest raiding—acting as a persistent alarm signal that attracts the slave makers but causes panic and disperses the defenders. Regnier & Wilson thus used the term "propaganda" (confusing) pheromone, which is now classified as an allomone. Dufour's gland is also used by the North American slave maker *Polyergus breviceps*, as a source of offensive chemicals. Topoff et al (115) suggested that the content of the gland acts as a pacification or appeasement pheromone, decreasing the aggressive response of the host *Formica* workers during usurpation. Accordingly, the Dufour's gland of the queen decreases in size shortly after the queen has successfully usurped the host colony and has been adopted by its resident workers. In the European slave-maker species *P. rufescens*, too, the queen has a hypertrophied gland. Mori et al (92) and Visicchio et al (127) showed that the content of the gland drastically lowers the aggression response of *Formica cunicularia* workers against intruders in laboratory conditions. In agreement with Topoff's classification, these authors suggest that the secretion constitutes an appeasement allomone that presumably assists the queen in successful usurpation. The chemistry of the gland was first analyzed by Bergström & Löfqvist (13), revealing only HCs and terpenoids, but recent data by D'Ettorre et al (44) showed that this gland produces an abundance of esters, of which decyl butanoate composes 80% of the secretion (Figure 1*A*; see also 127 and 105). Using the queenlike synthetic mixtures, these authors observed that the secretion reduces aggressive behavior in the *F. cunicularia* host workers. They hypothesized that the secretion may in fact act as a repellent to the host species rather than as an appeasement allomone. Indeed, decyl butanoate was shown to be a powerful repellent of the host worker, preventing even starved ants from imbibing a treated honey droplet. Interestingly, Dufour's gland secretions of workers are also fortified with esters, but these are of longer chain length with octadecyl butanoate as the major compound (Figure 1*B*). The secretion seems to be less effective as a repellent and does not have a marked effect in lowering the host's aggressive behavior (44). A complex mixture of acetates (mainly dodecyl acetate) and farnesene has also been identified in the Dufour's gland of *F. sanguinea*, but the role of these components has not been experimentally studied (3). Propaganda substances of the Dufour's gland are also used by the inquiline *Doronomyrmex kutteri* and the slave maker *Harpagoxenus sublaevis* during nest usurpation of the host *Leptothorax acervorum* (5, 95).

The Dufour's glands of queens of another slave maker, *Rossomyrmex minuchae*, also seem to play a role in nest usurpation. Before usurpation, these glands contain tetradecanal as a major product, which is almost nonexistent in queens that have been adopted by their host *Proformica longiseta*. This change lends credence to the hypothesis that the secretion functions as an offensive chemical that aids the parasitic queen to successfully usurp the host nest (H Hefetz, A Lenoir, F Ruano, & A Tinaut, unpublished data). The role of tetradecanal in invasion of the host colony by the *Rossomyrmex* queen remains to be studied.

CHEMICAL MIMICRY

Having invaded the host society, the parasite must be adopted or at least tolerated. To survive in the host colony, the parasite must to some degree be considered as a nestmate and accordingly must blend into the colony gestalt by achieving some degree of chemical congruency with the host. According to Howard (72) and Dettner & Liepert (41), there are two possibilities to obtain congruency: chemical mimicry (in which the parasite actively biosynthesizes the host cues) or camouflage (in which the parasite gets the cues from the host both by passive acquisition, for example, via contact with host and nest material, and by active acquisition, for example, via allogrooming and trophallaxis). Mimicry and camouflage are not mutually exclusive and can coexist in the same species. For example, Akino et al (2) showed that the caterpillar larvae *Maculinea rebeli* first biosynthesize the *Myrmica schencki* brood host recognition pheromones and later acquire from the ants additional HCs that mimic their host colony's odor. Because, in all cases,

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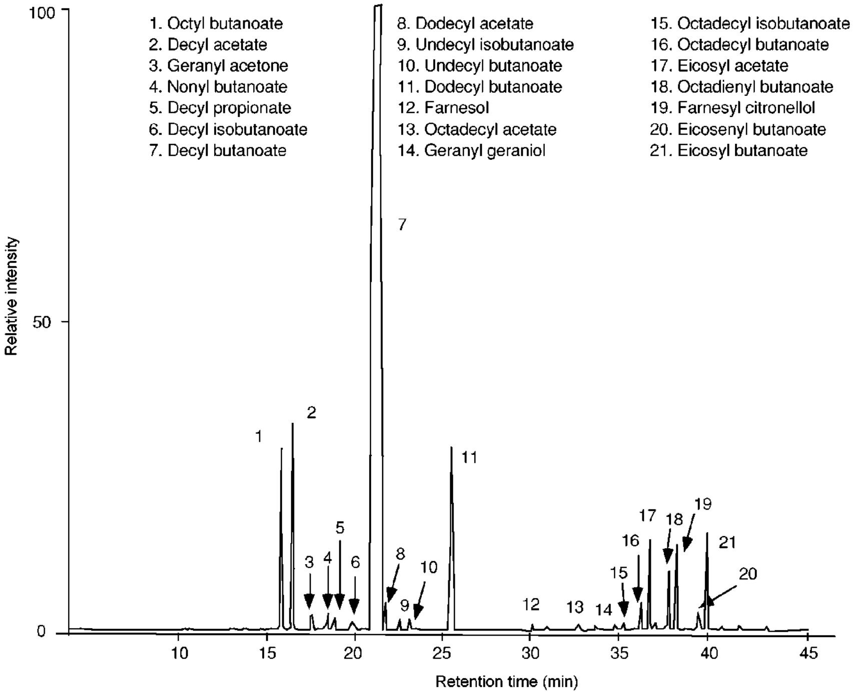
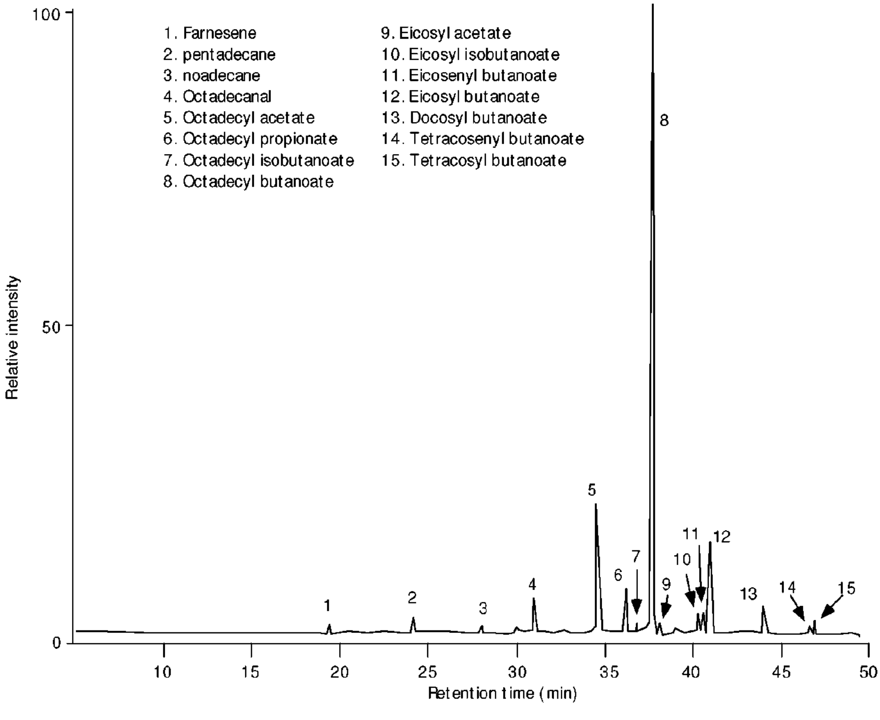
Figure 1 Gas chromatogram of *Polyergus rufescens* Dufour's gland secretion. (*A*) Queens before mating. (*B*) Workers (from 44, with permission of Birkauser).



A. The composition of Dufour's gland secretion of queen *Polyergus rufescens*



B. The composition of Dufour's gland secretion of worker *Polyergus rufescens* the parasite mimics its host odor, some authors, like Stowe (110), consider chemical mimicry only sensu lato, and we use this terminology.

Chemical Mimicry by Biosynthesis

Chemical mimicry by biosynthesis has been demonstrated (using radioisotopes) only in a few myrmecophile or termitophile insects. These include four species of the beetle *Trichopsenius* studied by Howard et al (71, 74), living in *Reticulitermes* nests, which have evolved the ability to biosynthesize the cuticular HCs of their host. The myrmecophile caterpillars of *M. rebeli* also biosynthesize specifically the HCs of the ant host *M. schencki*, and, as a consequence, they are rejected by other *Myrmica* species (2). The female syrphid flies of the genus *Microdon* lay their eggs at the entrance to an ant nest into which they are then transported by the host ants, and the larvae feed on ant brood. In *Microdon mutabilis*, Elmes et al (46) observed a strong maternal effect for egg adoption. Survival of the eggs reaches 95% when laid in the nest that reared the mother fly. It is hypothesized that the eggs are coated with an unknown chemical disguise that lasts 2 or 3 days after oviposition. The larvae of *Microdon piper* and *Microdon albicomatus* live with *Camponotus modoc* and *Myrmica incompleta* respectively, and, according to Howard et al (73), probably biosynthesize their host HCs. The adult flies, on the other hand, have different HCs and are immediately attacked by the ants if discovered in the nest.

Mimicry by Camouflage

Mimicry by camouflage seems to be the most common strategy species use to become integrated into the host colony. Host HCs can be acquired from the host, as it has been observed in myrmecophiles, termitophiles, and parasitoids (41, 85). Frequently, the parasites acquire the host odor by rubbing against the host or simply from the nest material. The colony odor is sometimes acquired through the consumption of ant larvae, as in the salticid spider *Cosmophasis bitaeniata* living in *Oecophylla smaragdina* nests (4). Chemical mimicry by camouflage has been intensively studied in the xenobiotic ant *Formicoxenus provancheri* and its host *M. incompleta* by Lenoir et al (85), who explained how the parasite can live peacefully inside the host nest. HC similarity between parasite and host was also found in the association of *Formicoxenus quebecensis* and *Myrmica alaskensis*. Adoption experiments revealed that the host odor is acquired during the first days of the adult life of the parasite and maintained later by intense host grooming (*F. provancheri* was called the "shampoo" ant by earlier authors). *Formicoxenus* foragers spend long periods in the host nest where ∼45% of their time is devoted to licking the host workers, of which 40% of this time is directed towards the host's head (83). Although the major purpose of this head licking is to obtain food, the parasite may also be attempting to obtain the PPG secretions. This may explain the special polyethism observed in *F. provancheri*, in which 75% of workers forage inside the host nest, which is exceptional in free-living ants (49). The newborn *Formicoxenus* workers have very low quantities of HCs, which provides a blank label that is rapidly filled with the host odor (A Lenoir, unpublished data). Moreover, it was also shown that *Formicoxenus* workers learn the host template at emergence (53). These two processes facilitate the chemical-mimicry process.

By contrast, *Formicoxenus nitidulus,* the guest ants of the *Formica rufa* group, do not present chemical congruency with the host (A Lenoir & A Hefetz, unpublished data). This ant species is less integrated within the host colony and may be considered more like a lestobiotic species. The genus *Formicoxenus* appears to comprise two behavioral groups of species: the first includes *F. provancheri* as real xenobionts with chemical mimicry; and the second includes *F. nitidulus*, which are simply guests of *F. rufa* group. Some behavioral records confirm this hypothesis; for example, *Formicoxenus diversipilosus* living in *Formica* nests is treated by the host with indifference (8, 59).

Inquilinism

The ultimate case of parasitism is inquilinism or permanent parasitism. Being rare in ants, it is the least studied chemically. The only known case is that of the cuckoo ant *D. kutteri* queens studied by Franks et al (60), which exhibit chemical congruency with their host *L. acervorum*. Congruency was shown with respect to both cuticular HCs and fatty acids, and the latter are also implied in nestmate recognition. Similar to the genus *Formicoxenus,* it is hypothesized that this congruency is the result of intensive grooming (60). Other inquilines may use the same strategy as has been anecdotally reported in some other cases, such as in *Teleutomyrmex schneideri,* whose queen frequently grooms the host queen (129).

By contrast, the chemical ecology of inquilinism was extensively studied in parasite wasps. Turillazzi et al (119) showed that the queen *Polistes sulcifer,* a parasite of *Polistes dominulus,* has a chemical signature before usurpation that differs from that of the host but that a matching process occurs as soon as 90 min after usurpation. The parasite queen deposits a mixture of HCs similar to that of the host colony on the surface of the nest, but it also deposits a unique compound (9, 15 dimethyl C_{29}). Therefore, *P. sulcifer* may exploit the host nestmate recognition system by changing the odor of the nest. In the association of *Polistes atrimandibularis,* parasite of *Polistes biglumis,* Bagnères et al (11) showed that the parasite is able to effectively manage its chemical signature. *P. atrimandibularis* queens enter the nest of the host and leave peacefully with the host queen. The cuticular profile of *P. atrimandibularis* queens changes according to the phase of parasitic association. Before usurpation, the wasps possess mostly unsaturated HCs on their cuticle. After establishment in the host nest, they cease producing the alkenes and progressively exhibit the host characteristic alkanes. At the end of the cycle, the queen slowly reverts to her original cuticular composition, that is, revealing progressively greater amounts of alkenes. Her descendents, on the other hand, have a mixture of alkenes and alkanes and can be readily distinguished from the mother queen. Why are the nonmimetic *P. atrimandibularis* offspring thus accepted into the host colony? Lorenzi et al (89) showed that, upon eclosion, both young parasites and young hosts lack a chemical visa, but the colony odor is soon acquired from the accepting colony (corresponding to our chemical-insignificance and chemical-integration periods). In addition, although residents of nonparasitized colonies recognize only the odor of their species, resident hosts of parasitized colonies learn a template that fits the odor of the two species.

Slavery

Chemical congruency in natural heterospecific colonies between slave-making ants and their slaves is known in a few species. Kaib et al (78) showed that the adult *H. sublaevis* slave makers adopt the *L. acervorum* or *Leptothorax muscorum* host odor. However, the situation is probably more complex, because Alloway & Keough (7) observed that *Protomognathus americanus* (the American species equivalent to *H. sublaevis*) insects chemically mark their slaves to prevent them from returning to their parental colony. According to Heinze et al (69), in *H. sublaevis* the slaves can belong to different species that may have different HC profiles and consequently a nonhomogenous colony odor. This incongruity between the heterospecific slaves leads to recognition errors and induces intracolonial aggression. *Chalepoxenus mullerianus* ants too sometimes have mixed slave species, but no chemical data are available (26). Another example of intracolonial aggression is induced by cestode parasites of *L. nylanderi*, which modify the cuticular odor of the ants, and consequently these parasitized workers are aggressed inside the colony by their sisters (118).

The Amazon Polyergus Ants In the Amazon *Polyergus* ants, the strategies appear to differ according to species. According to Yamaoka (130), the slave-keeper *P. samurai* ants do not synthesize the species-specific HCs, or they do so only in small amounts, but they obtain HCs from their slave workers, *F. japonica* or *Formica sp.5*. The European *P. rufescens* was studied by Habersetzer (64), Habersetzer & Bonavita-Cougourdan (65), and Bonavita-Cougourdan et al (16, 20). The enslaved *Formica rufibarbis* or *F. cunicularia* workers tend to lose their colony characteristics, but they do not adopt totally the HC profile of the genus *Polyergus*. On the other hand, *P. rufescens* cocoons from the same mother colony that were adopted by different *Formica* species (*F. gagates, F. cunicularia*, or *F. rufibarbis*) showed a cuticular profile that corresponded to the rearing species (P D'Ettorre, unpublished data; Figure 2), which indicates a mechanism for chemical camouflage.

D'Ettorre & Errard (42) have shown that alate virgin and newly fecundated *Polyergus* queens have very little HCs on their cuticle (Figure 3*a*). The invading strategy of *P. rufescens* queens makes use of their chemical insignificance. Being "odor invisible," the invading queens do not elicit overaggression in the host species. Moreover, they can deter *Formica* workers by repellent from their Dufour's glands (see above). Topoff & Zimmerli (116) and Le Moli et al (82) observed that when the *Polyergus* queen reaches the host queen, it bites her repeatedly and licks the

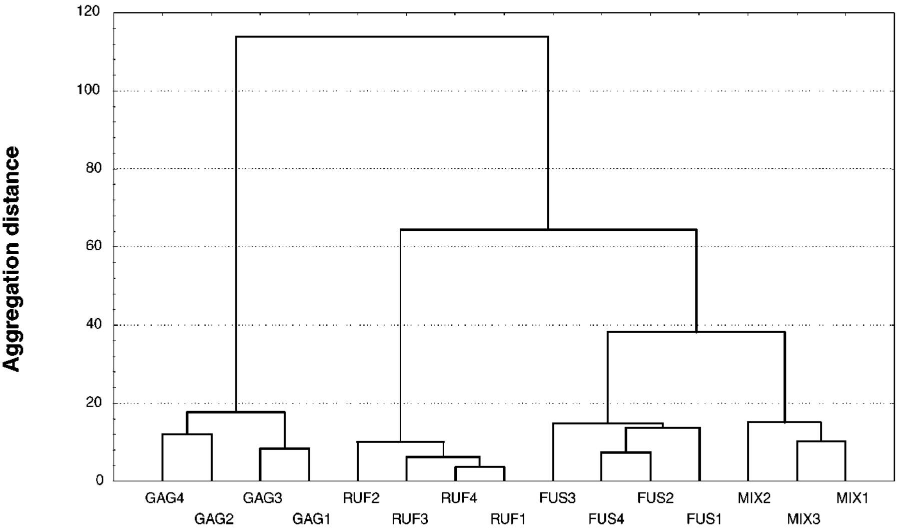
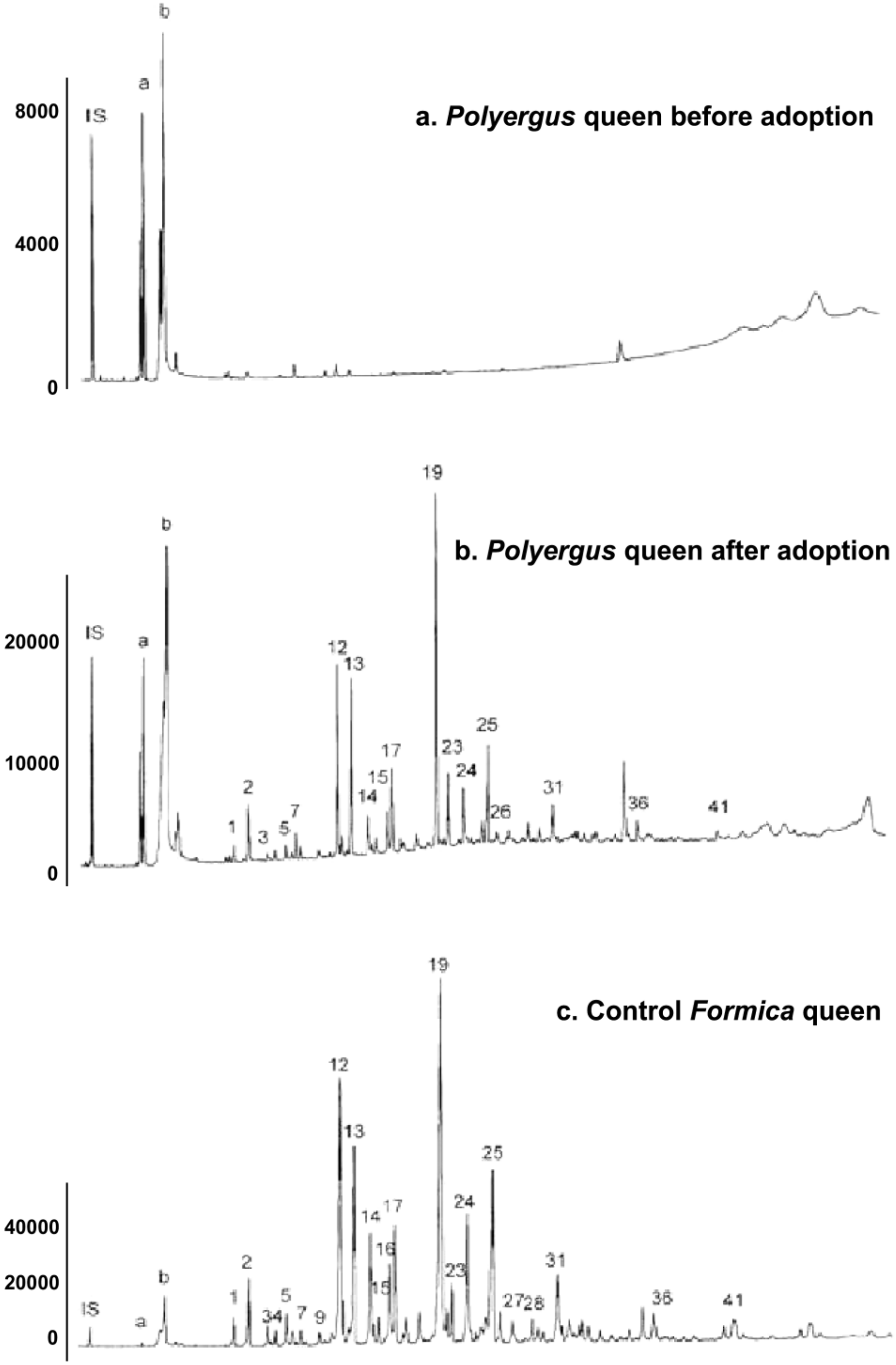


Figure 2 Hierarchical cluster analysis (Euclidean distance, Ward method) on cuticular hydrocarbons of *Polyergus rufescens* workers reared with *Formica gagates* (GAG); *Formica rufa* (RUF); and *Formica fusca* (FUS). MIX indicates workers in natural mixed colony with *Formica cunicularia* (P D'Ettorre, unpublished data).

dead queen's body extensively, probably to acquire its odor and be adopted by the workers (see also 6). This was chemically confirmed (Figure 3*b* and *c*). We suggest that the queen absorbs the host cuticular HCs into her PPG by allogrooming and later spreads it over her own body by self-grooming. Acquiring the host colony odor thus enables the queen to pass from the transient, chemically insignificant stage to the chemical-integration phase. It is interesting that the invading queens are more easily accepted into queen-containing than queenless colonies, presumably because they get chemicals typical of the mature queens (132). Whether this "odorless" strategy is used by other parasites is not known, but some observations indicate that it may be general. For example, the temporary parasite queens of *Formica pressilabris* remain in pupal position at the entrance to the host nest and are carried into the nest by the host workers, probably also owing to this chemical-insignificance strategy (see 70). Whether this poor HC representation on the cuticle of callow queens may be general in ants is an open question. Virgin queens of *C. niger* also have very low HC biosynthesis activity for ≤120 days postemergence (81). By contrast, *C. vagus* and *Lasius emarginatus* alates have normal HC profiles before swarming (17; A Lenoir & C Errard, unpublished data).

The Slave Maker Rossomyrmex Chemical congruency was also found between the slave-maker *R. minuchae*, endemic to Sierra Nevada (Spain), and its host


a. *Polyergus* queen before adoption
8000
4000
0
IS
a
b
b. *Polyergus* queen after adoption
20000
10000
0
IS
a
b
1
2
3
5
7
12
13
14
15
17
19
23
24
25
26
31
36
41
c. Control *Formica* queen
40000
20000
0
IS
a
b
1
2
34
5
7
9
12
13
14
15
16
17
19
23
24
25
27
28
31
36
41

P. longiseta. This qualitative congruency seems to be general (rather than nest specific) between the two species, because it was observed even between parasite and host from a nonparasitized alien nest. Quantitatively, however, these profiles are distinct. Worker *R. minuchae* probably pick up the scent of their host, but this remains to be studied (C Zamora-Muñoz, F Ruano, C Errard, A Lenoir, A Hefetz, A Tinaut, submitted for publication).

Because neither *Rossomyrmex* nor *Polyergus* spp. ever exist as free colonies, it is not surprising to find the above-described congruencies, indicating chemical mimicry. HCs of the facultative slave makers like *F. sanguinea* remain to be studied.

PERSPECTIVES

Kin Selection, Chemical Integration, and Evolution of Parasitism

According to Bourke & Franks (22), kin selection as the driving force for the evolution of insect societies also predicts strong selection for kin recognition. Schmid-Hempel (101) hypothesized that kin recognition also results from direct selection as defense against parasites. However, kin recognition in social insects is highly controversial and does not seem to be important even with respect to its manifestation in nepotism [except for queen rearing by honeybees (97)]. Robinson et al (100) hypothesized that nepotism cannot have a strong effect because it results in deleterious intracolonial conflicts. It has therefore been postulated that social bonding is based simply on nestmate proximity inside the nest. Accordingly, Jaisson (76) and Lenoir et al (84) suggested that kinship was replaced by fellowship or "nestmateship." Being more flexible than kinship, nestmateship is more prone to cheaters that attempt to bypass the nestmate recognition system. This strategy is not easy to achieve, as attested to by the numerous incidences of intracolonial aggression. Moreover the dynamic natures of label and template preclude a strategy whereby the parasite has a genetically based label-mimicking ability. Instead, it has to adopt the colony odor subsequent to usurpation. One solution for bypassing this system is that the cheater can introduce itself into

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Figure 3 (*a*) Gas chromatogram of a. *Polyergus rufescens* queen after mating and before adoption. (*b*) *Polyergus rufescens* queen after adoption in the *Formica cunicularia* host nest. (*c*) *F. cunicularia* queen from a monospecific colony. (modified from 42, with permission of the authors). Peak numbers: IS, internal standard, a, b: fatty acids, 1, C23:1; 2, C23; 3, 9+11 Me C23; 4, 7 Me C23; 5, 5 Me C23; 7, 5,13 dimethyl C23; 9, C24; 12, C25:1; 13, C25; 14, (9)+11+13 Me C25; 15, 7 Me C25; 16, 5 Me C25; 17, 3 Me C25; 19, 5,11+5,13 dimethyl C25; 23, C27:1; 24, C27; 25, 11+13 Me C27; 26, 7 Me C27; 27, 5 Me C27; 28, 9,11+11,13 dimethyl C27; 31, C28:1; 36, 11+13+15 Me C29; 41, 11+13 Me C31. Other peaks are present only in workers.

the colony during the chemical-insignificance period. The short duration of this period and the high vulnerability of the individual at this developmental stage are constraints that interfere with the evolution of such a system. We agree with the assertion of Lorenzi et al (89): “We may imagine that during evolution the non-expression of colony identity at emergence was one of the conditions that permit intra- and interspecific social parasitism.” In these conditions, it is not surprising that innate mimicry has not evolved, since the host odor is in all of the studied cases simply acquired by camouflage. We have seen that innate mimicry of colonial odor evolved only in some myrmecophiles, but in social parasites it is limited to alarm substances, for example, in *Bothriomyrmex* spp. (87). In this respect, colony identity based on individual recognition according to the individualistic model of colony odor may be more resistant to cheating and may explain why intercolonial adoptions as well as mixed colonies are so difficult to obtain when ponerine ants are involved (51, 76). In *Ectatomma tuberculatum*, Fénéron (55) observed that alien workers introduced as cocoons are initially adopted, but they are eventually rejected after several weeks. Likewise, foreign cocoons of the archaic Myrmeciinae ant genus *Myrmecia* are accepted, but after eclosion the callow workers are killed (30, 66, 76). We postulate that in these two subfamilies adoption is possible due to the chemical insignificance of the callows, but later on when the adopted ants biosynthesize their own HCs, they become progressively alien in the adoptive colony. Fresneau & Errard (61; see 84) also hypothesize that in ponerines the template is based simply on the bearer’s own HC profile. In such a personal chemical-reference system, the cost of parasitism may be too high to be selected, which may explain the absence of parasites in ponerines and myrmeciines.

Emery’s Rule

In 1909, Emery observed a remarkable morphological similarity between many parasites and their host species. He suggested that the two are probably phylogenetically related, with a common history and evolving from a common ancestor [“Emery’s rule” (47)]. Two hypotheses have been presented to explain this similarity. According to the social-deception hypothesis, the parasites may have evolved among closely related species because this facilitates the queen’s exploitation of the host intracolony-communication systems and subversion of colony-recognition mechanisms. According to the immediate-common-ancestry hypothesis, social parasites have evolved directly from their hosts, for example through intracolonial raids. For Schmid-Hempel (101), Emery’s rule has been globally reinforced in all studied groups. In ants, Emery’s rule has been supported by rRNA analyses (12) and enzyme patterns (67). On the other hand, there are a few cases in which cladistic analyses do not support the hypothesis that social parasites are most closely related to their host, for example, in wasps based on allozyme studies (28) and in ants based on morphological studies [e.g. *Pseudomyrmex* (128) and *Cataglyphis* (1)]. Nevertheless, we argue that the interpretations of these analyses are not completely convincing and do not really contradict Emery's rule, because in all these cases both hosts and parasites are classified in the same subfamilies or tribes [also as indicated by A Tinaut (personal communication)]. Recently, a case of inquilinism was discovered by Maschwitz et al (90) in *Polyrhachis lama* (Formicinae), a parasite of the genus *Diacamma* (Ponerinae) in Java. The authors hypothesized that this kind of parasitism between distantly related species might have evolved from visual mimetic relations between *P. lama* and the pugnacious *Diacamma* species. It would be interesting to verify whether cuticular chemical similarity in this case too facilitates deception. Additional support for the chemical-deception hypothesis is the finding that *Polyergus* species raid only *Formica* species from the *Serviformica* subgenus, but they never raid species in the *F. rufa* group. *F. sanguinea* sometimes also raid *F. rufa* group ants, but, at least under laboratory conditions, this leads progressively to emancipation of the slaves (35). This may be explained by the great chemical differences between the slave makers and *F. rufa* group. Moreover, in the field, *P. rufescens* do not raid *F. gagates* (82), probably because these ants of the *Serviformica* subgenus have an HC profile very different from the other members of the group, even if experimental adoptions are possible, as indicated above (P D'Ettorre, unpublished data). The case of *Formicoxenus* is a good example of this necessary chemical convergence. As predicted, the construction of mixed colonies of *F. provancheri* and a *Formica* species was unsuccessful (A Lenoir, unpublished data). It is noticeable that *F. nitidulus* in the laboratory can be reared in the absence of the host in mixed colonies with *L. acervorum*, which is a close species, but not with *Formica* species (24). On the other hand, Errard & Jaisson (51) showed that the formation of artificial mixed colonies is dependent on the phylogenetic distance between the species, and therefore this difficulty may be explained at least partly by the chemical distance between the species. In mixed colonies of *F. selysi-M. rubida*, integration of the two species is not complete and results in a pseudosocial colony (29), possibly owing to an important chemical distance between the two species, with *Formica* having large quantities of alkenes, whereas, in *Manica*, the cuticular profile is dominated by alkanes and lacks alkenes (10).

Coevolutionary Arms Race

Parasite ants and their host species are predicted to engage in a coevolutionary arms race, but no data are available regarding the mechanisms used by the host to prevent parasitism or whether the host modifies its behavior after previous encounters with the parasite. Davies et al (39) suggested several strategies by which ant hosts could theoretically defend themselves against parasites. These include better recognition of nonconspecific ants, immunity to appeasement substances, better fighting ability, and improved ability to discriminate self from non-self broods. However, there are few indications to date that species susceptible to parasitism display such features to a lesser extent than resistant species.

The observation that social parasites are more abundant in the colder regions of Europe and North America led to the hypothesis that cold climates predispose ant species towards parasitism by dulling the host's combativeness to parasite attacks, but the mechanism remains unexplained (70, 129). Recent observations on the slave maker *R. minuchae* and its host *P. longiseta* revealed that an allopatric parasite-free subpopulation of *P. longiseta* exhibited higher aggression towards the parasite than the parasitized subpopulation, independently of the differences in HC profiles (C Zamora-Muñoz, F Ruano, C Errard, A Lenoir, A Hefetz, A Tinaut, submitted for publication). This behavioral response may be an intrinsic character of the parasite-free subpopulation, and it may represent the development of a "behavioral immunity" to parasite attack, thus excluding the parasite from this area. It is the first indication in social insects of a strategy enhanced by a potential host against a social parasite, as hypothesized by Davies et al (39).

CONCLUSIONS

The chemical ecology of interactions between ants and their social parasites is a very promising field for research because it constitutes a variety of complex interactions, yet it has been little studied. The chemical weapons of the Dufour's gland are probably used by most of the slave makers and lestobiotic ants to combat their host, but the mechanisms by which it operates are still under debate. Do they act as propaganda/appeasement allomones or more simply as repellents? Chemical congruency between parasite and host is necessary to maintain cohesion in the mixed society. In all of the studied cases, the parasites mimic the host colony odor by means of disguise mechanisms. We know very little about the chemical ecology of the most advanced parasite species in which workers have completely disappeared. These may have evolved to achieve a true innate mimicry system.

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