

The result of an arms race: the chemical strategies of *Polistes* social parasites

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The ability of social insects to discriminate between nestmates and aliens on the basis of scent has been the selective pressure favoring the evolution of chemical strategies to facilitate integration into host nests by social parasites, i.e., by organisms which rely on the nests and workers of others to rear their brood. As a result of the coevolutionary arms race, obligate social parasites of *Polistes* wasps have evolved complex mechanisms of mimicry. Social parasites mimic host chemical signatures at the level of species, colony, and possibly rank. Social parasites possess diluted recognition cues and apply compounds to the host nests that may result in host manipulation. The origin and evolutionary pathway to host/parasite chemical similarity is discussed by making comparisons with the tactics used by facultative social parasites, and with the development of the cuticular signature in free-living species.

Introduction

When organisms of one species depend exclusively on organisms of another species — as occurs with parasites and their hosts — reciprocal selective pressures may result in the evolution of matching traits. For example, this may result in evolutionary trajectories where the antagonists in the arms race are selected to exhibit progressively more complex adaptations that facilitate parasitism, on one hand, and allow hosts to limit parasite exploitation on the other (Davies *et al.* 1989, Thompson 1994, 2005). In social insects, the close coevolutionary relationships between social parasites and their hosts has led parasites to evolve a number of mechanisms to overcome host barriers to colony invasion. Most of the studies on social parasite adaptations

to their parasitic lifestyle focus on deception, i.e., the ability to break the recognition code of hosts to penetrate host colonies (Holldobler & Wilson 1990). Such studies have documented that social parasite odors match the odors of the host species (Dettner & Liepert 1994, Lenoir *et al.* 2001). The analysis of the chemical adaptations of social parasites is fecund, and papers have described the subtle mechanisms leading to host mimicry, which occur soon after host nest entrance or even before their first encounter.

However, research has rarely focused on the origin and evolution of deceptive mechanisms used by social parasites. To this aim, the social wasps of the genus *Polistes* may represent a model system, mainly because the number of species of *obligate* social parasites within the genus is limited to only three, all of which share

a similar parasitic lifestyle. As a result, the scenario of obligate parasitic strategies is relatively simple in *Polistes* wasps. In contrast, *facultative* social parasitism is widespread in the genus (see Cervo & Dani 1996) and involves both intra- and inter-specific parasitic strategies, possibly covering a wide spectrum of integration mechanisms. The combined effect is that the *Polistes* genus offers the possibility to identify potential intermediate steps and prerequisites in the evolution of the adaptations to parasitic life.

The aim of this paper is to review the chemical adaptations of *Polistes* wasp social parasites, to treat them as adaptive parasitic traits, and to highlight their complexity (level of species, colony, rank). I will analyze the mechanisms involved in adopting cuticular signatures that match those of hosts, the timing and schedule for this process, and — by making comparisons with the tactics used by facultative social parasites and with the ontogeny of chemical signature in free-living *Polistes* species — investigate the possible origin and evolutionary pathways to host/parasite chemical similarity. Throughout the paper, the focus will be on the parasite queens, rather than on their brood, i.e. on those individuals that enter uninfested colonies, force hosts into tolerating them and later into caring for their brood, get colony control, and live in host colonies for months. The knowledge of these processes would permit the development of a scenario of the evolution of social parasitism in *Polistes* social wasps.

The barrier to invasion by aliens: nestmate recognition in *Polistes* free-living species

Within social groups of animals, insect colonies are particularly well-demarcated social units. Social insects usually make almost no mistakes in distinguishing between colony members and non-members, and strictly limit the admittance into their colonies to nestmates. This sophisticated ability depends mainly on chemoreception. As a general rule, social insects learn their colony odor rapidly after emergence and from that moment they are able to recognize nestmates from non-nestmates. They tolerate individuals

whose chemical signatures match the learned template and attack those which differ.

Recognition mechanisms are particularly well-known in *Polistes* wasps, due to the studies by Gamboa and co-workers (reviewed in Gamboa [1996, 2004]). Pfennig *et al.* (1983) documented abilities of *Polistes* wasps to develop recognition within four hours after emergence, and that this process occurs correctly only if wasps spend their first hours on their nests or on fragments of their nests. When newly emerged wasps perceive nest paper odor they are later able to match the learned template with the “odor” of the cue bearer (Pfennig *et al.* 1983, Gamboa *et al.* 1986). Thus the comb has a central role in the process of learning recognition odors in *Polistes* wasps. As in other social insects, recognition cues in *Polistes* paper wasps are complex species-specific blends of hydrocarbons which cover the insect cuticle (epicuticular hydrocarbons) and the surface of the comb (Lorenzi *et al.* 1996, Singer 1998). Epicuticular blends are similar within members of the same colony (Lorenzi *et al.* 1996, Singer 1998), and between the comb and the resident wasps (Singer *et al.* 1998). In social wasps, the epicuticular layer is generally a blend of methylated, branched and linear hydrocarbons; their variations in quality usually identify the species, their variations in quantity within a fixed composition identify the colony to which insects belong.

As a result, each colony (comb and adults) has a unique chemical signature, which allows chemical nestmate/non-nestmate discrimination. In social wasps, recognition experiments have shown that epicuticular hydrocarbons are sufficient to allow correct nestmates/non-nestmate discriminations (Dani *et al.* 1996, Lorenzi *et al.* 1997, Cervo *et al.* 1996, Ruther *et al.* 1998; but also Lahav *et al.* [1999] in ants).

Thus research confirms that *Polistes* wasps have sophisticated recognition abilities. This is the reason why it is surprising to observe in the wild that all intruder wasps are promptly rejected from alien conspecific colonies, but social parasites, which belong to alien species or colonies, can infiltrate host colonies. Although most studies on nestmate recognition have been accomplished on only seven *Polistes* species (Gamboa 2004), there is no reason to think that the host

species (*P. dominulus*, *P. gallicus*, *P. biglumis*, *P. nimphus* and *P. associus*) of obligate social parasites do not exhibit recognition abilities. And indeed, evidence exists that two of the host species discriminate colony members from non-nestmates (*P. biglumis*: Lorenzi *et al.* [1997], Lorenzi [2003]; *P. dominulus*: Dani *et al.* [1996], Starks *et al.* [1998], and indirectly, Sledge *et al.* [2001b]).

The contrast between the ability of paper wasps to discriminate between nestmates and aliens, and that of obligate parasites to deceive host barriers with intruders, has stimulated much research aimed at elucidating the adaptations of social parasites to their lifestyle.

The wasp social parasites

Polistes wasps have three species of obligate social parasites that share a distribution area (Mediterranean and Caspian basin, Cervo [2006]), and an ancestor (Choudary *et al.* 1994), but use different main hosts (Scheven, 1958, Cervo & Dani 1996, Fanelli *et al.* 2001). In addition, they have similar lifestyles. Parasite females enter the host nests after natural nest foundation by the host foundresses, usually before the emergence of the host brood (Scheven 1958, Cervo *et al.* 1990a, Turillazzi *et al.* 1990, Mead 1991, Zacchi 1995, Zacchi *et al.* 1996). However, *Polistes* parasites employ different — either non-violent or aggressive — behavioral strategies for usurpation (Cervo *et al.* 1990a, Cervo & Dani 1996). After having defeated their hosts with a violent attack or with a sneaking strategy, parasites subdue subordinate females and subdue or chase out the legitimate resident queen. Each parasite queen controls a single host colony, possibly up to the end of the colony cycle. Once they are established in the invaded colonies, parasite “queens” begin egg-laying and dominate resident hosts. In *Polistes* obligate parasites, parasite eggs develop either into gynes or males: no parasite workers are produced. Thus, parasites rely on the comb and the workforce of host species for reproduction.

In contrast to bird brood parasites, which lay eggs in host nests and leave, insect social parasites enter host colonies and establish themselves there for long periods, which, in *Polistes* wasps,

may coincide with the end of active colony life (Cervo, 1990, Lorenzi *et al.* 1992). When parasites have taken over host colonies, they participate in colony life, i.e. they lay eggs and inspect cells but they also interact with hosts, receive food from them, and behave as dominant individuals, without overt rebellion from hosts (but see Dapporto *et al.* 2004). This indicates that the parasites use long term strategies to trick hosts, and that adaptations to parasitic life are even more complex than in parasitic birds (Davies *et al.* 1989). Indeed, insect social parasites exhibit adaptations in both immature stages which develop in host nests (*see* Cervo 2006) and adult parasite females which enter host colonies and live there for months. Adult parasite females exhibit morphological traits (thickened cuticle and robust mandibles, for example) which favor overcoming the physical defense that hosts oppose when parasites enter host nests (Cervo 1994). However, in *Polistes* as in the other social insect parasites, one of the most intricate, intriguing and most studied adaptations is the range of chemical strategies employed by parasites, which have the function of achieving integration with resident hosts, tricking hosts into tolerating usurpers and into allocating colony resources to parasites.

Parasites intercept the host chemical code of recognition: chemical strategies of integration

Social parasites overcome species-specific differences in recognition cues by chemical adaptations defined as mimicry or camouflage of host odor (reviewed by Dettner & Liepert [1994], Lenoir *et al.* [2001], Howard & Blomquist [2005]), i.e. by exhibiting a chemical resemblance with hosts. When the process of resemblance is attained, parasites exhibit epicuticular profiles with host-specific compounds in host-specific proportions, possibly passing through a blank state or chemical insignificance (Lenoir *et al.* 2001).

Mimicry at the level of species

In all three species of obligate parasites of

Polistes wasps, parasites integrate within host colonies by chemically mimicking the hosts (here, mimicry is used as a general term for chemical resemblance, without referring to the origin of the compounds involved, Dettner & Liepert [1994]). Indeed, Bagnères *et al.* (1996) described that *P. atrimandibularis* females are chemically quite distinct from their *P. biglumis* hosts before host nest invasion — at that time, their cuticular hydrocarbon blend contains parasite-specific compounds, the alkenes, which are lacking in the hosts. After host nest invasion, chemical analyses show that alkenes decrease in the parasite epicuticular profiles and that the parasite cuticle becomes enriched with those compounds abundant in the host chemical signature. One month after invasion, when the host brood emerges, parasite females are chemically indistinguishable from their hosts (Table 1).

Similar patterns occur in the other *Polistes* social parasites. For instance, the matching processes of epicuticular hydrocarbons in *P. sulcifer* begin soon after entering the host nests (Turillazzi *et al.* 2000) and *P. semenowi* matches their host colonies 2–4 weeks after entering them (Lorenzi *et al.* 2004a). In all three cases, mimicry is accurate; parasites lose, where present, parasite-specific hydrocarbons and acquire host-specific hydrocarbons (Table 1).

Mimicry at the level of colony

Polistes obligate social parasites also match the

host colony chemical signature (Sledge *et al.* 2001b, Lorenzi *et al.* 2004a), so that each parasitic female is accepted as a nestmate by host residents, but is rejected in other colonies of the same host species (Sledge *et al.* [2001b] for *P. sulcifer*; Lorenzi [2003] for *P. atrimandibularis*, where recognition of parasites as nestmates was tested in the field). Besides *Polistes* social parasites, mimicry of individual host colony's odor was rarely documented (i.e. in the butterfly *Maculinea rebeli*, a social parasite of ants, Akino *et al.* [1999]; and in a myrmecophilus spider, Elgar & Allan [2004]) although it is probably a common feature in parasites that deceive hosts whom exhibit nestmate recognition abilities.

Mimicry at the level of rank

Colony-specific matching of host cuticular odors may not be all accomplished by social parasites. Dapporto *et al.* (2004) documented that *P. sulcifer* female parasites exhibit the chemical profile of the alpha rather than that of the beta female after invading *P. dominulus* nests (even when the alpha female was removed before parasite invasion). This deception, if it is such, is complete, and host workers use only visual cues to unmask their parasites.

The “dominant cuticular profiles” may be used by subordinate foundresses and by workers as indicators of egg-laying capacity of the dominant individuals (Sledge *et al.* 2001a). This may ensure the acceptance of an egg-layer by workers

Table 1. Chemical mimicry in *Polistes* obligate social parasites. ? = no data available; – individuals not present.

		Similarity between parasite and hosts			
		Before host nest invasion	Soon after host nest invasion	After co-inhabiting with hosts (host workers emerge)	End of colony cycle (parasite brood emerge)
<i>P. atrimandibularis</i> ⁽¹⁾	Parasite females	no	no (but less divergent than before)	yes	no
	Parasite adult brood	–	–	–	no
<i>P. sulcifer</i> ⁽²⁾	Parasite females	no	yes*	yes	?
<i>P. semenowi</i> ⁽³⁾	Parasite females	no	?	yes	?

* Host workers can emerge either before or soon after host nest invasion (Cervo 1990).

Data from: ⁽¹⁾ Bagnères *et al.* 1996; ⁽²⁾ Turillazzi *et al.* 2000; ⁽³⁾ Lorenzi *et al.* 2004.

(Dapporto *et al.* 2004), as the removal of alpha females causes competition over reproduction in *Polistes* colonies (reviewed in Reeve 1991). The exhibition of an alpha profiles by parasites may thus favor parasite control over host reproduction (which occurs in *Polistes*, Cervo & Lorenzi [1996]).

However, evidence that subordinate foundresses and workers use the alpha cuticular profile as a signal is still lacking (Dapporto *et al.* 2004). If it is found, it will be further confirmation that acute discrimination abilities by hosts have created severe selection pressures for parasites that mimic hosts in the smallest details.

Concealing identity via a blank state

In the two species of *Polistes* social parasites where specific analyses were done, usurping females were poor in cuticular hydrocarbons with respect to their hosts (Lorenzi & Bagnères 2002, Lorenzi *et al.* 2004a). This peculiarity was previously noted in ant social parasites (Lenoir *et al.* 2001), but may be a general property of social parasites' chemical signatures. Indeed, authors often report that parasites possess cuticular chemical profiles "simpler" than those of their hosts, but quantitative data on cuticular lipids are not often available, or the sampling method do not allow the quantification of the total cuticular lipids per insect (e.g. Turillazzi *et al.* 2000).

The critical role of epicuticular hydrocarbons is that of limiting dehydration (Gibbs 1998, Howard & Blomquist 2005). Social parasites share the same habitat with their hosts, and even the same colony, and thus probably have similar physiological hydration requirements. Given that social parasites possess lower quantities of epicuticular hydrocarbons than their hosts, parasite

scarcity in recognition cues could be the result of specific selective pressures operating on social parasites.

Polistes atrimandibularis social parasites have only about 20%–60% of the amount of epicuticular hydrocarbons of their *P. biglumis* hosts for most of their life (Lorenzi & Bagnères 2002). The deficiency in epicuticular hydrocarbons with respect to hosts is extreme in parasite queens when they invade host nests (the amount in parasites is 22% of the amount in their hosts, Table 2), but significant differences with the amount of their hosts are maintained during the whole colony cycle. Only at the end of colony cycle, when parasite queens stop egg laying and their similarity with the host vanishes (Bagnères *et al.* 1996), does the quantity of parasite queens' cuticular lipids increase (and largely exceeds that of the hosts). At the end of colony cycle, when parasite brood emerge, parasite female adult offspring (which will behave as parasite queens next summer) were significantly poorer in epicuticular lipids than their hosts. In this parasite species, the scarcity of cuticular hydrocarbon is a consistent property of adult females, with the only exception of old queens at the end of their life.

Data available for *P. semenowi* show a similar pattern (Lorenzi *et al.* 2004a) (Table 2). Parasite females possessed only 40% of the amount of epicuticular hydrocarbons of their *P. dominulus* hosts before entering host nests but had 60% two–four weeks after invasion.

During winter, parasites and hosts possibly hibernate in different habitats, as parasites perform altitudinal migration and hibernate up in the mountains at elevations higher than their hosts (Cervo & Dani 1996). Dehydration risks, however, increase with altitudes. Thus overwintered parasites, which abandon their high-mountain hibernacula and search for host nests in

Table 2. Variation in the total quantity of hydrocarbons in *Polistes* obligate social parasites.

Parasite species	Mean amount of hydrocarbons (% with respect to hosts)		
	at host-nest invasion	mid-colony cycle	end of colony cycle
<i>P. atrimandibularis</i> * Parasite females	22%	58%	290% (old queens) 70% (adult female offspring)
<i>P. semenowi</i> ** Parasite females	40%	60%	

* with respect to *P. biglumis* (Lorenzi & Bagnères 2002). ** with respect to *P. dominulus* (Lorenzi *et al.* 2004a).

lowland or at lower altitudes, should exhibit even larger amount of cuticular hydrocarbons than their hosts. Which selective pressures may have instead favored such a scarcity of cuticular lipids?

Possessing small amounts of epicuticular compounds might facilitate the acquisition of host odors after nest invasion (Lorenzi *et al.* 2004b), if the cuticle more easily absorbs exogenous compounds when the lipid layer is less abundant. Indeed, newly emerged wasps are poor in cuticular lipids, and acquire hydrocarbons from the nest or the artificial environment in the first hours after emergence (Panek *et al.* 2001, Lorenzi *et al.* 2004b). In the same way, the total amount of hydrocarbons increases in parasites after the invasion of host colonies (Lorenzi & Bagnères 2002, Lorenzi *et al.* 2004a), but it never reaches 100% of the amount detectable in hosts (Table 2). Thus, it is possible that the scarcity of lipids favors the acquisition of compounds from host nests in social *Polistes* parasites, but available information does not fully support this hypothesis.

The scarcity of cuticular lipids in social parasites may be used to conceal identity. This hypothesis was initially formulated to explain a similar phenomenon in social parasites of ants (Lenoir *et al.* 2001). The concept is that, as cuticular lipids constitute chemical signatures in recognition processes, a dilution of such cues may render the identification of a cue bearer more difficult. In the case of social parasites, a dilution of recognition cues may favor acceptance by hosts. In favor of this hypothesis is the observation that young wasps (which possess poor quantities of hydrocarbons) have free access in alien colonies soon after emergence, but are rejected later, when the amount of their cuticular hydrocarbons has increased (Lorenzi *et al.* 1999, Panek *et al.* 2001, Lorenzi *et al.* 2004b). Newly emerged *P. atrimandibularis* females are not an exception, and they are tolerated by host residents in alien parasitized nests during their first hours of life (but rejected from un-parasitized nests, suggesting that, although poor in recognition cues, they possessed parasite-specific compounds that were unfamiliar to wasps from non-parasitized nests) (Lorenzi *et al.* 1999). Also in favor of this hypothesis, is the observation that resident wasps

do not reject non-nestmate dead wasps when they have had their hydrocarbons removed by solvent-washing (Dani *et al.* 1996, Lorenzi *et al.* 1997, Sledge *et al.* 2001). Here, the lack of recognition cues inhibits aggressive responses by residents.

However, notwithstanding the minimum amount of cuticular compounds, parasite queens are recognized and attacked by host residents at nest invasion. Moreover, they exhibit the potential dilution of recognition cues even after reaching complete mimicry with host colonies. These two observations partially counter the hypothesis that parasites conceal their identity by means of a dilution of recognition cues. Perhaps the amount of hydrocarbons required to be fully “chemically invisible” is even smaller than the amount possessed by parasites, and the quantity of recognition cues they have only help parasites partially inhibit host aggressive reactions or to avoid detection. This hypothesis needs further analyses. It is possible that chemical mimicry operates with a deficiency in recognition cues to limit identification of parasites as intruders into host colonies, thus facilitating the integration process and minimizing fatal discrimination by hosts.

The timing of mimicry

A few species-specific peculiarities may be found in the pathways that lead *Polistes* obligate parasites to match the chemical signature of their hosts.

The epicuticular profile of *P. semenowi* female parasites was not qualitatively much different from that of its *P. dominulus* hosts before host nest invasion (Lorenzi *et al.* 2004a). No parasite-specific compounds were found in this species and parasites needed no more than fifteen days to match the profile of the individual host colony that they invaded.

Before *P. sulcifer* invaded nests of the host species *P. dominulus*, a single parasite-specific compounds was found on their epicuticular layer, although large differences distinguished the profiles of hosts and parasites. Specifically, the odor of the parasite was simpler than that of the host, lacking a number of compounds that were present in the host profile. As early as 90 min after host-nest invasion, the first variation in the parasite epicuticular blends began, and the

parasite cuticle became enriched in host-specific compounds. Major changes were completed by 3 days after host nest invasion, and at that point, the differences between parasite's and host's odors were not larger than those between the hosts themselves (Turillazzi *et al.* 2000).

In the field-collected samples of *P. atrimandibularis*, the profiles of the parasites were qualitatively different from that of its *P. biglumis* hosts before host nest invasion and showed entire classes of parasite-specific compounds (Bagnères *et al.* 1996). Within 6 days after host nest invasion, the chemical signatures of the parasites began to converge with those of the hosts: unsaturated hydrocarbons, which were the parasite-specific compounds, disappeared from the cuticle and host-specific compounds began to be present. However, although changes occurred soon after nest usurpations, the complete matching of the host recognition cues required about 30 days so that it was reached when host workers began to emerge from invaded nests (Bagnères *et al.* 1996, M. C. Lorenzi unpubl. data).

Available data suggest that in the three species of social parasites, the larger the difference in the chemical profile of parasites and hosts, the longer it takes parasites to match the recognition cues of their hosts. However, selective forces may modulate the speed of the host-matching processes. In all three species of social parasites, mimicry is reached approximately when workers emerge from colonies (Table 1), suggesting that mimicry may be crucial to control host workers. Host worker emergences can occur soon after host nest invasion in *P. semenowi* and *P. sulcifer*, but a month later in *P. atrimandibularis* (Cervo 1990, Lorenzi *et al.* 1992). At least in *P. atrimandibularis*, parasites completely subdue host foundresses without matching their chemical profiles (Bagnères *et al.* 1996).

Integration without mimicry (the peculiar case of old parasite queens and their adult brood)

Surprisingly, chemical resemblance with hosts it is not the only chemical strategy that ensures acceptance by hosts. The chemical profiles of the adult brood of *P. atrimandibularis* and *P. sulcifer*

contain parasite-specific hydrocarbons (Bagnères *et al.* [1996], in large amounts in *P. atrimandibularis* male brood, Lorenzi *et al.* [1996], Turillazzi *et al.* [2000]), although the adult parasite's brood inhabits host colonies and hosts tolerate them. Species-specific profiles probably favor mate searching and identification, but also make parasites detectable in host colonies.

In *P. atrimandibularis*, recognition tests showed that newly emerged parasite females were accepted in any parasitized colony, but were rejected in non-parasitized colonies of the host species (Lorenzi *et al.* 1999), although they were only accepted in their natal host colonies when they matured (Lorenzi 2003). Thus, parasite offspring emerge with parasite-specific labels (which cause rejection from non-parasitized colonies), but without colony-specific labels (allowing acceptance in any parasitized colonies) (Lorenzi *et al.* 1999) which they acquire later (Lorenzi 2003). However, the parasite brood is accepted in natal colonies notwithstanding the fact that they possess parasite-specific hydrocarbons. These contradictory results can be understood because *Polistes* wasps learn their colony odors from the nests. Parasites manipulate colony odors by supplementing the paper nest surface with parasite-specific compounds (Lorenzi & Bagnères 1996, Lorenzi *et al.* 1996, Turillazzi *et al.* 2000). When host workers emerge in parasitized colonies, they experience the supplemented colony odor and later accept emerging parasite brood with parasite-specific labels, as well as nestmate hosts with host-specific labels (Lorenzi *et al.* 1996). Here, contamination of host colonies by parasite-specific cues mediates parasite acceptance by hosts.

How are chemical adaptations attained?

Behavioral mechanisms

Specific behaviors are possibly involved in the variation of the lipid layer of the cuticle. Both *P. sulcifer* and *P. semenowi* parasites stroke their abdomens on the nest surface soon after entering the host nest (Turillazzi *et al.* [1990], Zacchi [1995], but *see* also Cervo & Dani [1996] for

the same behavior in *Polistes* facultative parasites). In social wasps, nest paper is covered by a hydrocarbon layer similar to that of resident wasps (Lorenzi *et al.* 1996, Singer *et al.* 1998), so that physical contact between parasite cuticle and nest hydrocarbons may favor the transfer of odors between wasps and comb. In parasites which quickly mimic host odors, like *P. sulcifer* and *P. semenowi*, stroking may favor fast acquisition of host hydrocarbons from the comb surfaces. Indeed, stroking is rarely performed by *P. atrimandibularis*, where mimicry is achieved over an extended period.

Besides stroking, social parasites lick their hosts and eat eggs and immature host brood (Turillazzi *et al.* 1990, Cervo *et al.* 1990b). These behaviors may favor ingestion and accumulation of host hydrocarbons by the parasites, contributing — possibly with biochemical modification within the parasites — to matching the chemical signature of hosts. However, no studies have specifically addressed the problem of the origin of the compounds involved in the process of mimicry. The question remains open as to whether *Polistes* social parasites acquire host-specific compounds passively from hosts, biosynthesize them, or if both processes occur. A halt in the production of parasite-specific compounds, as well as the absorption of colony-specific compounds, were both supposed to occur in *P. atrimandibularis* (Bagnères *et al.* 1996) and in *P. sulcifer* (Turillazzi *et al.* 2000, Sledge *et al.* 2001b).

Hydrocarbons involved in the variation of the chemical signature

The analysis of chemical variation in the hydrocarbon blend should theoretically help in the identification of the compounds (or classes of compounds) directly involved in the nestmate recognition process. In honeybees only particular hydrocarbons within the cuticular chemical profile are used as recognition cues (Breed 1998) and the same may occur in social wasps (Espelie *et al.* 1990, Dani *et al.* 2001, Lorenzi *et al.* 2004b). In social parasites, the compounds which are present on the parasites before usurpation, but disappear later (parasite-specific hydrocarbons), are candidates for compounds perceived by resident

wasps and used for rejection of aliens from home colonies. The compounds acquired by parasites after nest invasion are candidates to be perceived by resident wasps and used as cues contributing to the acceptance of nestmates. As such, these analyses are expected to clarify the recognition process. However, variation in the chemical composition of parasite epicuticular hydrocarbons are so large that it is difficult to distinguish between them. For example, Lorenzi *et al.* (2004a) in *P. semenowi* listed the hydrocarbons acquired by parasites 15–30 days after entrance in the nest of the host species *P. dominulus*. During this period, the parasites exhibit about 20 new hydrocarbons on their cuticles, all branched hydrocarbons (except three linear alkanes) of 25 to 35 carbon each. As these hydrocarbons were already present in the chemical signature of hosts before usurpation, they may have been acquired from hosts or nests. Currently, the variation is too large to give clues to the nature of the chemicals involved in the identification process. The only consistent finding is that all three parasite species become enriched in long-chain compounds after host nest usurpation (*P. atrimandibularis*: Lorenzi & Bagnères unpubl. data, *P. semenowi*: Lorenzi *et al.* 2004a; *P. sulcifer*: Dapporto *et al.* 2004) and that high quantities of long-chain hydrocarbons distinguish dominant *P. dominulus* females from workers (Dapporto *et al.* 2004).

Other adaptations to parasitic life: manipulation of host recognition abilities?

In *Polistes* colonies parasitized by social parasites, resident hosts may encounter nestmates with two different recognition labels: namely, nestmate hosts and parasite queens with host-specific cuticular odors, and adult parasite brood with parasite-specific cuticular odors. Recognition tasks of host workers may thus be more complex than in un-parasitized colonies. Indeed, less efficient recognition abilities in parasitized nests were documented in *P. biglumis* colonies parasitized by *P. atrimandibularis* (Lorenzi 2003). Similar results were obtained in ants, where workers from polygynous ant colonies were less discriminant towards aliens than work-

ers from monogynous colonies (Sundström 1997, Starks *et al.* 1998, Vander Meer & Alonso 2002). A tendency to make recognition errors may also be seen in *P. biglumis* and *P. nimphus* colonies usurped by conspecific females (M. C. Lorenzi *et al.* unpubl. data). Here, usurped workers do not attack alien females significantly more often than their foundresses or usurpers. The common variable in all those studies is the fact that nests were usurped or have multiple queens. It is possible that in such colonies two recognition labels coexisted, thus making the process of learning of recognition cues more complex and making the ability to discriminate between nestmates and non-nestmates less efficient.

Parasites and usurpers, as non-related colony members, may benefit from impaired host recognition abilities (*see* Keller 1997) and might actively scramble recognition cues by depositing appropriate chemicals on host combs. The tainting of the nest surface with parasite-specific compounds was reported in *P. atrimandibularis* (Lorenzi *et al.* 1996, Lorenzi & Bagnères, 1996) and in *P. sulcifer* (Turillazzi *et al.* 2000). Here, parasite cuticles contained alkenes (in *P. atrimandibularis*) or 9,15-dimethyl C₂₉ (in *P. sulcifer*) before usurpations, and these compounds were found on nest paper after usurpation (while their amount decreased drastically in parasites). In this case, the transfer of chemical cues may serve to remove or alter information about kinship. Research on the variation of nest odor in parasitized and usurped colonies has rarely been performed, but in many cases the experimental procedures that document mimicry by parasites or usurpers cannot exclude the possibility that parasites or usurpers do not deposit chemicals on invaded nests. Indeed, studies that analyze this aspect prove that invaded combs are contaminated by the intruders' odors (Lorenzi & Bagnères 1996, Lorenzi *et al.* 1996, Turillazzi *et al.* 2000).

A property of adult parasite cuticular signature: plasticity

Polistes social parasites vary their chemical signature until it matches that of their hosts, but variation still occurs after the matching of the nests

has been completed (Bagnères *et al.* 1996). This variation occurs in adult individuals and indicates that the chemical signatures of parasites are dynamic in both their qualitative and quantitative composition. Free-living adult *Polistes* wasps do not change individual chemical signatures when they leave the nest to forage or when they visit alien colonies to steal food (behavioral evidence documents that they are accepted into their colonies after performing these activities, M. C. Lorenzi [unpubl. data]). Moreover, free-living *Polistes* wasps maintain their species-specific chemical signature even when they live in parasitized colonies with parasite brood or when their nest paper is covered by unsaturated parasite-specific compounds (chemical evidence, Bagnères *et al.* [1996], in *P. biglumis*). Indeed, adult *Polistes* wasps of free-living species do not change their cuticular patterns when they are experimentally exposed to hydrocarbons (behavioral and chemical evidence, Lorenzi *et al.* [2004b], in *P. dominulus*). In contrast, newly emerged wasps of free-living species do change their epicuticular chemical composition drastically after emergence. *Polistes dominulus* females emerge with a chemical profile which is poor in recognition cues and within 3 days the quantity of cuticular hydrocarbons triples. Moreover, soon after emergence, the cuticle of young wasps absorbs hydrocarbons when exposed to alien nests (Lorenzi *et al.* 1999) or to natural quantities of hydrocarbons (Lorenzi *et al.* 2004b). In this respect, the epicuticle of newly emerged wasps resembles that of mature parasites: both are poor in recognition cues and both absorb hydrocarbons from the environment (for free-living species: Panek *et al.* [2001], Lorenzi *et al.* [2004b]; for *Polistes* social parasites: Lorenzi & Bagnères [2002], Lorenzi *et al.* [2004a]; for a review of the same phenomenon in ants: Lenoir *et al.* [2001]). Here, the ontogeny of chemical signatures gives insight into the possible origin of mimicry in social parasites.

Chemical strategies of facultative social parasites: acquisition of host colony odor or marking host combs?

In *Polistes* wasps, the foundresses of the free-

living species are able to behave as facultative social parasites (Cervo & Dani 1996). In the field, data on the success of usurpation by facultative parasites often indicates that colonies fail (low usurped nest productivity: Klahn 1988, Cervo & Lorenzi 1996b, Cervo & Dani 1996) and instances where emerging host workers unmask the usurpers are reported. Worker rebellion is often observed in usurped wasp colonies (worker/usurper aggressions: Klahn 1988, Lorenzi & Cervo 1995, Cervo *et al.* 2004; usurper egg destruction by workers: Makino 1988; workers with well-developed ovaries, Cervo & Turillazzi 1989, Dani *et al.* 1994; nest desertion by workers: Cervo & Lorenzi 1996b). Thus, in nature, workers do not always accept usurpers. In contrast, reports on overt failures of colonies usurped by *Polistes* obligate parasites is rare (but see Dapporto *et al.* 2004). This suggests that adaptations to the parasitic lifestyle are efficient for the obligate parasites, but may be less efficient for facultative parasites. Thus, investigating the mechanisms of infiltration displayed by facultative parasites may provide insight into the first step along the evolutionary pathway to efficient chemical mimicry.

Until recently, no experiment had tested how facultative usurpers integrate within the host colonies, but two hypotheses have been discussed in the literature: facultative *Polistes* parasites were thought to apply their own odor to host combs or to acquire host odors from host combs.

The specialized facultative parasite *P. nimphus*

Recently, Rita Cervo and I investigated the chemical strategies used by usurpers entering alien nests by employing an experimental procedure that can best be described as cross-fostering between colonies (Lorenzi *et al.* 2006). We examined *P. nimphus*, the only *Polistes* wasp which is known to usurp both conspecific and heterospecific colonies successfully (Cervo *et al.* 2004). While conspecific nest usurpation is common in free-living *Polistes* wasps, heterospecific nest usurpation is rare (Cervo *et al.* 2004). In the phylogeny of obligate social parasites, *P. nimphus* belongs to the sister group of the obligate social parasites (Choudary *et al.*

1994). In our view, the ability of *P. nimphus* to usurp heterospecific colonies, the fact that they possess morphological adaptations for parasitic life (Cervo *et al.* 2004), and that the species shares a common ancestor with obligate parasites, renders *P. nimphus* the most intriguing species in which to study chemical adaptations to facultative parasitic reproductive options.

In *Polistes* wasps, conspecific nest usurpation occurs during the pre-worker phase (Reeve 1991), when foundresses are the only adults that can contribute to the colony's chemical signature. In *Polistes* colonies in the post-worker phase, all colony members may contribute to the production of colony odor (Turillazzi *et al.* 2000).

Experimental data show that *P. nimphus* usurpers employ different chemical integration methods depending on the host species. *P. nimphus* females mimicked the odor of conspecific host colonies (as obligate social parasites do), but were unable to mimic host odors when hosts were heterospecifics. In this case, *P. nimphus* usurpers marked heterospecific host nest with their own odor. These results suggest that *P. nimphus* exhibit some parasite-like traits, such as absorbing compounds on their cuticles, but these traits are not as efficient as in obligate social parasites. The chemical signature of each colony is probably unique in *P. nimphus* (no experiment has shown that, but see Turillazzi *et al.* [1998], Lorenzi & Caprio [2000]), but chemical differences are usually larger between species than between conspecific colonies (Howard & Blomquist 2005). Results are consistent with the hypothesis that usurpers overcome colony-level differences in the chemical signature by mimicking conspecific host-colony odor, but do not overcome species-specific differences when usurped nests belong to heterospecifics.

The facultative parasite *P. biglumis*

The ability to mimic the chemical signature of conspecifics by facultative *Polistes* parasites may not be universal. *Polistes biglumis* is a free-living species where foundresses may behave as facultative usurpers by invading conspecific nests, but no evidence indicates that foundresses are able to usurp heterospecific nests. Results of

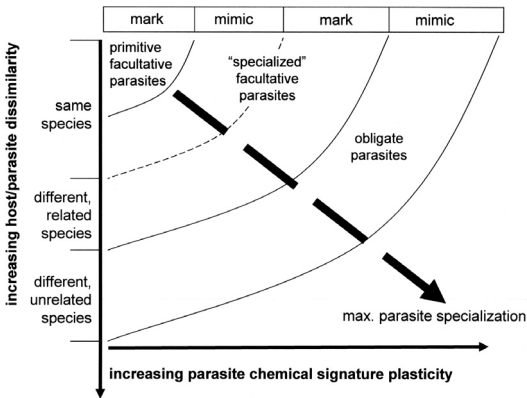


Fig. 1. Schematic diagram showing the hypothetical evolutionary steps of the chemical strategies employed by social parasites for integration into host colonies. In this evolutionary pathway, expanded plasticity in the chemical signature is a specialized trait, favoring successful integration into those host nests that belong to species less phylogenetically related. The terms “mark” or “mimic” refer to the chemical strategy employed by parasites (mark: parasites mark host nests with their own odor; mimic: parasites mimic host colony odors).

recognition tests in conspecific usurped colonies indicate that in this species usurpers do not mimic conspecific host colony odor, but rather mark host nest with their own odors (M. C. Lorenzi *et al.* unpubl. data). If similar tests in other free-living species give consistent results, the evolutionary scenario might be that facultative parasitic species are generally incapable of mimicking alien colonies and instead they mark them. The exception might be *P. nimphus* and the other free-living species which successfully usurp both con- and hetero-specific colonies in the wild: *P. apachus* (Snelling, 1952), *P. metricus* (Hunt & Gamboa 1978), *P. canadensis* (O'Donnell & Jeanne 1991) *P. lanio* (Giannotti 1995) and possibly *P. dominulus* (Cervo & Dani, [1996], R. Cervo pers. comm., but see Cervo *et al.* [2004] for the success of usurpations).

Conclusions

Obligate parasitism evolved from intra-specific parasitism via inter-specific parasitism (Davies *et al.* 1989, Taylor 1939, Cervo & Dani 1996, Cervo 2006). As shown in Fig. 1, a plausible evolutionary pathway to chemical mimicry in

Polistes wasps begins with the primitive chemical strategy of facultative usurpers that taint conspecific host nests with their own odor (as documented in *P. biglumis*, M. C. Lorenzi *et al.* [unpubl. data]). Applying odors to host nests may allow the usurper to be accepted by its own brood, but not necessarily by host brood. At high conspecific parasitism pressures, the ability of host workers to unmask usurpers (and reproduce directly) will be favored.

At each step in the evolution of chemical strategies of usurpation, the rebellion of host workers (which can kill usurpers or eliminate their eggs; Klahn 1988, Makino 1988, Lorenzi & Cervo 1995, Cervo *et al.* 2004) may represent strong selective pressure favoring more efficient chemical strategies of usurpation. At this point in the evolution of chemical mimicry, usurpers that contaminate their own cuticles with conspecific host nest odors may have been selected for, as such usurpers were able to hide their true identity from host workers. This occurs in *P. nimphus* usurpers invading conspecific nests (Lorenzi *et al.* 2006).

Usurpers can be foundresses which leave their hibernacula late in the spring or which have lost their previous nests (Cervo & Dani 1996). It is important to note that females isolated from nests and nestmates lose exogenous components of their odor (Gamboa *et al.* [1986] as cited in Gamboa [2004]). It will be interesting to determine if usurpers, which lack nests, are poor in exogenous compounds. If scarcity in recognition cues is a pre-requisite for the acquisition of chemicals from the environment (as suggested by the properties of young wasps and mature parasites; see Lorenzi *et al.* 1999, Panek 2001, Lorenzi *et al.* 2004b, Lorenzi & Bagnères 2002, Lorenzi *et al.* 2004a), usurpers might possess poor cuticular blends and absorb the exogenous components of odors when exposed to alien nests.

So far I have only discussed conspecific usurpation; in this case chemical differences between usurpers and host nests are small variations in relative proportions within the same qualitative hydrocarbon composition. Within a population, conspecific usurpers only acquire colony-specific proportions of compounds that they already have. The required degree of plasticity of the chemical signature is limited.

A further step in the evolution of social parasitism is thought to be inter-specific parasitism. Here, *P. nimphus* may represent the next step. In this species, usurpers successfully invade nests of other species and laboratory simulations indicate that, in contrast to their ability to mimic conspecific host odors, *P. nimphus* usurpers only deposit their own odor on heterospecific nests. Again, applying their own odor seems to be the easiest and the most accessible chemical strategy, which is used when chemical differences are larger than between conspecific colonies.

One step further in the arms race to trick hosts, obligate *Polistes* parasites are consistently poor in recognition cues prior usurpation, and are able to match the host colony chemical signature after usurpation. This is accomplished even when hosts belong to different and distantly related species. Here the chemical signature is so dynamic and plastic that parasites can halt the production of parasite-specific compounds and change drastically the composition of their profiles, notwithstanding the large differences with the host species. Obligate parasites probably have not lost the ability to apply compounds to host nests, but rather employ both that tactic and their ability to resemble hosts chemically to their advantage.

Although the data available at the moment suggests that the three species of obligate social parasites employ very similar chemical strategies, this is may not be true. *P. atrimandibularis* is a generalist and invades nests of four different host species which partially live in sympatry (Fanelli *et al.* 2001, Cervo 2006). Recent analyses on microsatellite loci exclude the possibility that these parasites form genetically distinct host races (Fanelli *et al.* 2005). Thus an extreme plasticity of chemical mimicry mechanisms appears to be the only adaptation responsible for such diversity of hosts. Thus, it will be extremely interesting to examine the chemical strategies that *P. atrimandibularis* employs with different hosts, and to try to understand the ecology of parasitism of this species. Here, the co-evolutionary arms race may be played between a parasite and many different antagonist host species at the same time.

At the moment, such a scenario for the evolution of chemical mimicry is reasonable, but still needs confirmation, although clues exist

for a few of these steps. New observations will be necessary to develop a better understanding of the evolution of the chemical strategies in this group. Increasing our understanding of the mechanisms of parasite infiltration into host colonies will contribute to a greater understanding of co-evolutionary processes between social parasites and their hosts.

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