

# The chemical strategies used by *Polistes nimphus* social wasp usurpers (Hymenoptera Vespidae)

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*Polistes* foundresses can behave as facultative social parasites when, instead of founding their own nest, they usurp colonies of the same or a different species and temporary use the host workforce to raise their own brood. Conspecific usurpation appears to be common among *Polistes* wasps, but nothing is known about the mechanisms that these facultative social parasites use to have themselves accepted within usurped colonies. Using behavioural tests, we studied the chemical strategies employed by females of *Polistes nimphus* when they behave as facultative social parasites in colonies of the same or of a different species. We hypothesized that usurpers would mark host nests with their own odours and/or acquire host nest odours in order to camouflage their real identity from host workers. Our results indicated that *P. nimphus* usurpers used different chemical strategies depending on host nest species: they acquired conspecific host odours but marked heterospecific host combs with their own odours. © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, 91, 505–512.

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## INTRODUCTION

Brood parasitism is a reproductive tactic that arises when individuals avoid caring for their young and rely on other individuals (of their own or another species) to perform these activities. Social parasites are brood parasites in social insect colonies: they rely on the workforce of other queens to raise their own brood. Much research has analysed the mechanisms that obligate social parasites (individuals unable to build their nests and rear their own brood) use to deceive host workers and integrate in host colonies. The term ‘chemical mimicry’ describes the chemical strategy commonly used by obligate social parasites in host colonies. Indeed, social parasites have odours different from their hosts before entering host nests, but parasites are chemically undistinguishable from their hosts after the invasion of host colonies (Dettner & Liepert, 1994; Lenoir *et al.*, 2001). In organisms that

largely base recognition processes on chemoreception, it is likely that chemical mimicry favours the acceptance of parasites as nestmates by resident hosts.

In social insects, little attention has been paid to the integration mechanisms of facultative social parasites (i.e. individuals that can either build or usurp nests) where intermediate traits between nonparasitic and parasitic organisms may be present. Research here lends insight into the possible origin and evolutionary history of parasitic behaviour.

In paper wasps of the genus *Polistes*, free-living social wasps may found nests by themselves or behave as social parasites by usurping colonies of the same or of another species (Cervo & Dani, 1996; Cervo, 2006). Although facultative nest usurpation appears to be widespread among the *Polistes* genus (Cervo & Dani, 1996), virtually nothing is known about the mechanisms that facultative parasites use to integrate in the usurped colony. In *Polistes* wasps, nestmate recognition is based on odours, and emerging females learn the odour of their nests and nestmates from their natal

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combs. Each female will use this odour template to discriminate between nestmates and alien individuals they meet (Pfennig *et al.*, 1983; Gamboa, 1996; Gamboa, Reeve & Pfennig, 1986a; Gamboa *et al.*, 1986b). Epicuticular hydrocarbon blends are the cues responsible for nestmate recognition. The composition of epicuticular blends differs between species and, within a species, is more similar between members of the same colony than between individuals belonging to different colonies (Lorenzi *et al.*, 1996, 1997; Singer, 1998).

When facultative nest usurpers invade host nests, they are chemically different, in terms of odour, from the colony that they usurp. Therefore, natural selection has favoured females that minimize the difference between their own odour and the host comb odour. This may occur through acquisition of host odours by usurpers and/or through the application of usurpers' odours to host colonies. *Polistes* obligate social parasites acquire host odours (Bagnères *et al.*, 1996; Turillazzi *et al.*, 2000; Lorenzi *et al.*, 2004; Lorenzi, 2006) and are accepted as nestmates by resident hosts (Sledge *et al.*, 2001; Lorenzi, 2003). Although the mechanism by which facultative usurpers integrate within usurped colonies has not been experimentally tested, in *Polistes* social wasps, conspecific usurpers are thought to achieve integration with the host colony by applying their own odour to the host nest surface (Klahn, 1988; Cervo & Turillazzi, 1989; Dani, Cervo & Turillazzi, 1992a,b; Gamboa, 1996; Jeanne, 1996). Other studies have suggested that usurpers mimic host odours (as obligate social parasites do) by acquiring components of host colony odours from host combs (Lorenzi & Cervo, 1992; Dani *et al.*, 1994; Cervo & Dani, 1996; Cervo & Lorenzi, 1996; Cervo *et al.*, 2004).

Abdominal stroking is the behaviour that may be involved in the passage of odours from the usurper cuticle to the host comb or vice versa (Dani *et al.*, 1992a, b): this behaviour is frequently performed by both facultative usurpers and obligate social parasites after their arrival on host nests (Cervo & Dani, 1996; Cervo & Lorenzi, 1996; Cervo *et al.*, 2004). Dani *et al.* (1992a) proposed that wasps apply chemical substances to nests when they stroke their abdomen on nest paper. In a recent study, Van Hooser *et al.* (2002) investigated the function of abdominal stroking in *Polistes fuscatus* in the context of intraspecific usurpation. The results of their study were consistent with the hypothesis that, during abdominal stroking, the queen usurpers apply recognition cues to the comb surface.

In the present study, we investigated the chemical integration strategy of *Polistes nimphus* (Christ) a facultative usurper. In *P. nimphus*, intraspecific usurpation is common: 19% (three of 16) and 27% (six of 22) of nests were usurped in two different years, usurpa-

tion occurring in solitary foundations during the pre-worker period (Cervo, unpubl. data). *Polistes nimphus* can also successfully usurp the nest of the sympatric species *Polistes dominulus* (Christ) and behave as an interspecific parasite, a strategy rarely observed in other free-living *Polistes* species (Cervo *et al.*, 2004). Moreover, this species belongs to the sister group of the obligate social parasites (Choudary *et al.*, 1994) whose ancestors might have played a key role in the evolution of social parasitism in the genus *Polistes* (Cervo *et al.*, 2004; Cervo, 2006). *Polistes nimphus* is thus an ideal model for the study of the origin and evolution of social parasitism in wasps.

We performed two sets of experiments using the same experimental protocol and investigated the chemical tactics employed by overwintered nest-founding *P. nimphus* females (foundresses) when they usurped nests of the same or different species (intraspecific and interspecific usurpation experiments). We tested whether *P. nimphus* usurpers applied odours to host nests or acquired odours from host nests.

## MATERIAL AND METHODS

### COLONY COLLECTION

We collected 107 solitary foundations of *P. nimphus* and 50 solitary foundations of *P. dominulus*, in May to June, in different locations in Tuscany and Piedmont (Italy). All colonies were in the preworker stage. Colonies kept in the laboratory were caged in cubic glass boxes (15 × 15 × 15 cm) and maintained under a natural 12 : 12 h light/dark photoperiod with electric lighting. Honey, water and *Tenebrio molitor* larvae were supplied *ad libitum*.

### INTRASPECIFIC EXPERIMENTS: *P. NIMPHUS* PARASITIZING *P. NIMPHUS*

Thirty-four *P. nimphus* nests were cut into halves with scissors, with each half-nest containing a similar number of pupae. During nest cutting, foundresses were kept in small containers. One half of each nest was caged in a box with its original foundress, whereas the other half was placed in another box with an alien conspecific foundress removed from her colony (for this, we used another 34 of the *P. nimphus* colonies collected) (Fig. 1). Thus, of each nest, one half was reared by its original foundress (F-nest, control) and the other half was offered to and reared by a foreign female (U-nest). In this way, for each manipulated nest, we simulated the arrival of an intraspecific usurper in one half. When females are induced to adopt a foundress-free pre-emergence colony, their role within the colony is comparable to that of a usurper (Klahn, 1988; Cervo & Turillazzi, 1989;

Lorenzi & Cervo, 1992). Conspecific usurping females were not related to the adopted colony: they were collected from nesting sites located at least 10 km apart.

#### INTERSPECIFIC EXPERIMENTS: *P. NIMPHUS* PARASITIZING *P. DOMINULUS*

As for the above set of experiments, we cut 39 *P. dominulus* nests into halves. For each nest, one half was reared by its original foundress (F-nest, control) and the other half was reared by a *P. nimphus* foundress (U-nest) removed from her colony (for this, we used the remaining 39 *P. nimphus* colonies collected) (Fig. 1). Therefore, both sets of experiments simulated events of facultative parasitism on U-nests (intraspecific in the first set and interspecific in the second set).

#### GENERAL PROCEDURE

In both experimental sets, foundresses and usurpers were left on their half combs for 4 days. Foundresses and usurpers were then collected, freshly killed by freezing, and kept frozen until recognition tests were performed.

We eliminated the few workers that emerged before foundress or usurper removal. All other workers, which emerged after foundresses or usurpers were removed from colonies, were subject to recognition tests (see below). As a result, before the recognition tests, tested workers had never met their foundresses, nor the usurping females.

In addition, 2 h of behavioural observations were performed on 24 *P. nimphus* and on 22 *P. dominulus* foundresses on their own nests before the experimental manipulation. After nest cutting, *P. dominulus* foundresses were observed again, this time on the half nests. *Polistes nimphus* usurpers were observed in the same manner. Behavioural data were used to evaluate differences in stroking behaviour before and after the experimental manipulation.

#### NUMBER AND CHARACTERISTICS OF TESTED COLONIES

We performed recognition tests only on colonies that had been successfully usurped, whose foundresses or usurpers were alive and active on the nests for the entire 4-day period. Each colony selected had at least one worker (emerged after foundress or usurper removal) that had not abandoned the natal colony and which was at least 24 h old (colony odour is learned within a few hours after emergence; Pfennig *et al.*, 1983; Gamboa *et al.*, 1986a). We eliminated data from both halves of the nests whenever one half did not meet the above criteria. The experimental manipulation and the strict criteria that we followed strongly reduced sample size (14 *P. nimphus* nests were selected in intraspecific experiments and 17 *P. dominulus* nests in heterospecific experiments). Table 1 shows the details of tested half nests.

Half colonies were tested at the very beginning of postemergence period (when one or few workers are present on the nests).

#### RECOGNITION TESTS

Recognition tests consisted of presenting workers from half nests cared for by foundresses (F-nests) and half nests cared for by usurpers (U-nests) with the specific females: (1) the original nest foundress; (2) the usurper (i.e. a fertile female from a distant location that had adopted an alien (intra or interspecific) half nest); and (3) an alien fertile foundress (of both species for interspecific experiments), which was collected from a site at least 10 km away, as control.

All these females were kept frozen in individual glass vials for  $8.1 \pm 3.3$  days (mean  $\pm$  SD) for intraspecific experiments and  $4.6 \pm 3.4$  days for interspecific experiments.

Tests were conducted in the laboratory; each test colony was presented with one female at a time. Each female was held by forceps, placed 1 cm from the anterior face of the nest, and kept there for 1 min from

**Table 1.** Species, sample size, type of tested half nests and their characteristics (mean number of cells and pupae) at the moment of nest cutting. The mean number of workers and their mean age at the time of the recognition experiments are also shown

Species of usurper (female)	Species of usurped colony	Type of half nest	Number of half nest	Number of cells (mean $\pm$ SD)	Number of pupae (mean $\pm$ SD)	Number of tested workers (mean $\pm$ SD)	Age of tested workers (mean $\pm$ SD)
<i>Polistes nimphus</i>	<i>Polistes nimphus</i>	F	14	22.46 $\pm$ 8.56	3.54 $\pm$ 3.02	1.88 $\pm$ 0.96	2.92 $\pm$ 1.44
		U	14	21.77 $\pm$ 9.22	3.31 $\pm$ 2.81	2.15 $\pm$ 0.99	3.13 $\pm$ 1.62
<i>Polistes nimphus</i>	<i>Polistes dominulus</i>	F	17	18.35 $\pm$ 7.27	2.77 $\pm$ 1.30	1.53 $\pm$ 0.53	2.26 $\pm$ 1.33
		U	17	21.46 $\pm$ 6.75	3.65 $\pm$ 1.58	1.38 $\pm$ 0.70	2.74 $\pm$ 2.07

F, half nest cared for by the foundress; U, half nest cared for by the usurper.

the moment of unambiguous reactions of the workers. Foundresses, usurpers, and alien fertile females were presented to each half colony in random order, at intervals of at least 10 min. Tests were blind and the observers did not know which wasp (foundress, usurper or foreign fertile female) was being presented.

We counted the number of intolerant behaviours (bites, attacks, leaving the nest, grasping, stings) exhibited by workers towards each presented female and then divided that by the number of workers on nest at the time of testing.

We expected that U-workers accepted their usurpers if usurpers had employed a chemical strategy of integration. Moreover, we expected to observe that, in the case where usurpers had acquired odours from the host nests, F-workers tolerated their sisters' usurpers; alternatively, if usurpers had marked the host nests, F-workers attacked their sisters' usurpers.

Wilcoxon test was used for statistical comparison, where paired data were sisters from foundress-reared and usurper-reared half nests. Exact *P*-values (two tailed) were used for small sample sizes (Mundry & Fischer, 1998).

## RESULTS

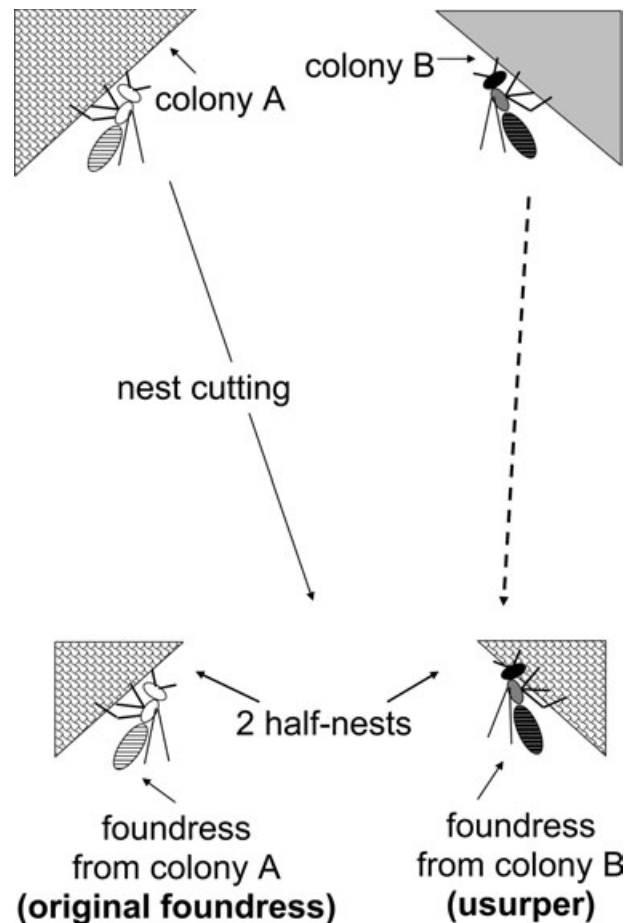
### INTRASPECIFIC EXPERIMENTS: *P. NIMPHUS* PARASITIZING *P. NIMPHUS*

Resident workers in F-nests (Fig. 2) were significantly more tolerant towards their original foundresses or their sisters' usurpers (which had never lived on the foundress-reared half-nests) than towards foreign females (Wilcoxon test, respectively,  $z = -2.26$ ,  $P = 0.024$ ;  $z = -2.387$ ,  $P = 0.017$ ) and did not distinguish between their mothers and their sisters' usurpers ( $z = -1.806$ ,  $P = 0.071$ ). This suggests that, during their 4-day stay on the half nests, usurpers had acquired compounds from the host nests.

Workers resident in U-nests (Fig. 2) did not discriminate between foreign females and their foundresses ( $z = -1.094$ ,  $P = 0.294$ ) or usurpers ( $z = -0.863$ ,  $P = 0.388$ ) or between their foundresses and usurpers ( $z = -1.154$ ,  $P = 0.248$ ).

### INTERSPECIFIC EXPERIMENTS: *P. NIMPHUS* PARASITIZING *P. DOMINULUS*

*Polistes dominulus* workers resident in F-nests were significantly more tolerant towards *P. dominulus* foundresses than towards *P. nimphus* usurpers of the other half of their nests ( $z = -2.42$ ,  $P = 0.016$ ) and foreign females of either species ( $z = -2.77$ ,  $P = 0.006$  for *P. dominulus* foreign females and  $z = -2.74$ ,  $P = 0.006$  for *P. nimphus* foreign females) (Fig. 3). Indeed, the reactions towards usurpers were not significantly dif-



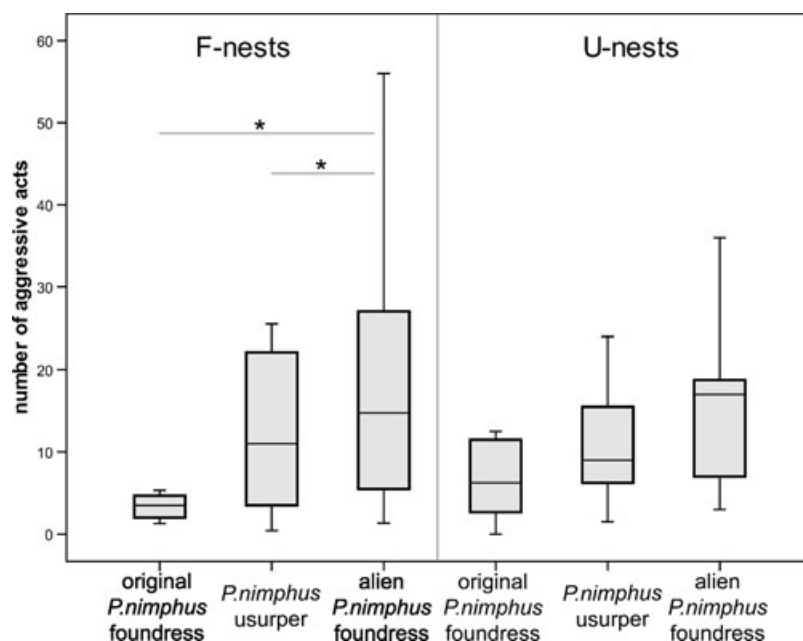
**Figure 1.** Nest cutting procedure used to divide a nest into two parts that would be cared for one part by the original foundress, the other by an alien female (referred to as the 'usurper').

ferent from those towards alien *P. dominulus* and *P. nimphus* females ( $z = -1.09$ ,  $P = 0.276$  and  $z = -1.63$ ,  $P = 0.102$ , respectively).

Workers from U-nests did not discriminate between their usurpers and their mothers ( $z = -0.76$ ,  $P = 0.449$ ) and were significantly more tolerant towards usurpers than towards foreign females of either species ( $z = -2.68$ ,  $P = 0.007$  for *P. dominulus* foreign females, and  $z = -3.24$ ,  $P = 0.001$  for *P. nimphus* foreign females) (Fig. 3). They were also more tolerant towards their mothers than towards *P. nimphus* foreign females ( $z = -2.95$ ,  $P = 0.003$ ) or *P. dominulus* foreign females ( $z = -3.05$ ,  $P = 0.0002$ ).

### BEHAVIOURAL OBSERVATION IN INTERSPECIFIC EXPERIMENTS

With respect to the observations of abdominal stroking, when the 22 *P. dominulus* foundresses were



**Figure 2.** The number of aggressive behaviours by resident *Polistes nimphus* workers to introduced dead foundresses (original *P. nimphus* foundress), intraspecific usurpers (*P. nimphus* usurper), and foreign females of the same species (alien *P. nimphus* foundress) in 14 foundress-reared half nests and in 14 usurper-reared half nests. Box plots show the 75th and 25th percentiles as boxes, the median as the lines in the box and the 95th and 5th percentiles as vertical lines. Significant differences between reactions are indicated by asterisks (\* $P < 0.05$ ).

returned to their half-comb after nest cutting, their stroking rates were not significantly different from those exhibited before the experimental manipulation (sign test,  $t = 4$ ,  $P = 0.377$ ). By contrast, when the 24 *P. nimphus* foundresses usurped *P. dominulus* half-nests, abdominal stroking on host nests was significantly more frequent than on their own nests before the experimental manipulation (sign test,  $t = 0$ ,  $P < 0.0005$ ).

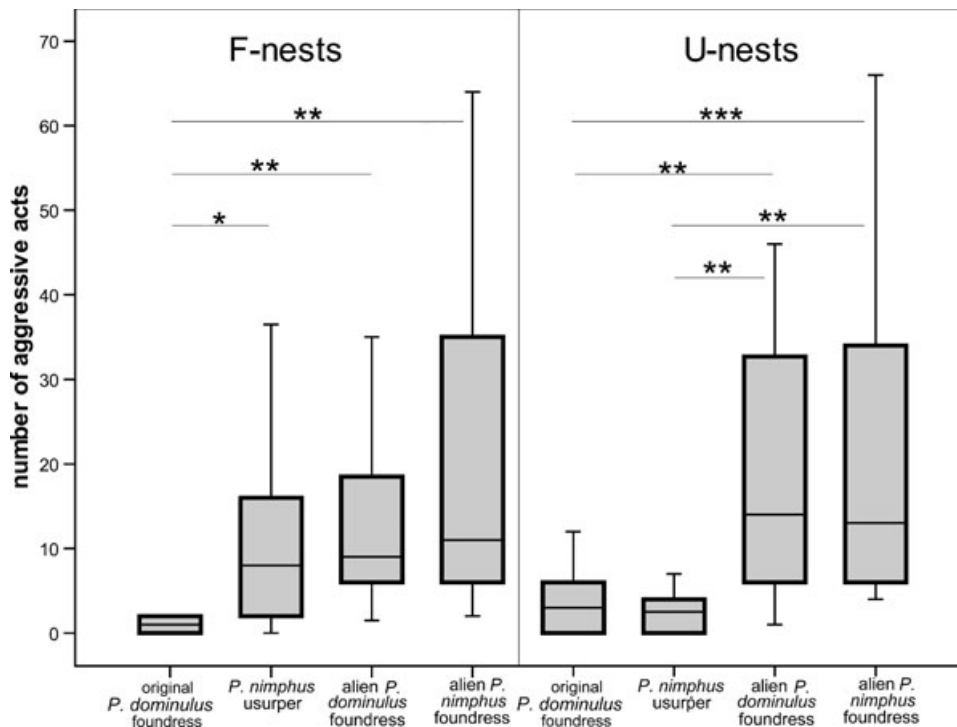
## DISCUSSION

The results of the present study show that facultative usurpers use a chemical strategy when they usurp host nests. Indeed, both in intra- and in interspecific usurpation experiments, workers from the usurped half-nests did not discriminate between foundresses and usurpers. However, this is not sufficient to clarify whether usurpers acquired odours from the host nests (mimicry; *sensu* Dettner & Liepert, 1994) or applied odours to the host nests.

The crucial experiment to distinguish which strategy is employed by usurpers was the introduction of usurpers into foundress-reared nests: if resident workers accepted the usurpers of their sisters as nestmates, then usurpers had acquired odours from the host nests; alternatively, if workers rejected the usurpers, then usurpers had applied their odours on the

usurped-nests without acquiring host nest odours. In our tests, usurpers were accepted by workers from F-nests in intraspecific experiments, but were attacked by workers from F-nests in interspecific experiments. Thus, in our experimental setting, the chemical strategy employed by usurping *P. nimphus* females changes and depends on host-nest species.

The results from the experiment that simulates intraspecific usurpation are obvious: usurpers were accepted as foundresses not only by workers in U-nests, but also by their sisters in F-nests. These data show that usurpers acquired the odour of the host colonies: in this way, when introduced into the foundress-reared half-nests, they were treated as nestmates. Thus, in conspecific nest usurpations, *P. nimphus* usurpers use the same chemical strategy as obligate social parasites. Here, the stroking behaviour performed by conspecific usurpers on host combs (stroking conspecific combs by usurpers is well documented; Cervo & Dani, 1996) may favour the contamination of usurper's cuticle with host odours. The experiments, however, cannot exclude that usurpers both mimicked host colony odours and marked host nests with their own odours. In these tests, workers from U-nests treated alien foundresses with equivalent levels of aggression, as towards their mothers and usurpers. Here, we can hypothesize that, when learning their recognition template at emergence, workers on



**Figure 3.** The number of aggressive behaviours by resident *Polistes dominulus* workers to introduced dead foundresses (original *P. dominulus* foundress), interspecific *P. nimphus* usurpers (*P. nimphus* usurper), and foreign *P. dominulus* (alien *P. dominulus* foundress) and *P. nimphus* (alien *P. nimphus* foundress) females in 17 foundress-reared half nests and in 17 usurper-reared half nests. Box plots are as described in Figure 1. Significant differences between reactions are indicated by asterisks (\* $P < 0,05$ ; \*\* $P < 0,01$ ).

usurped nests perceived more diverse recognition cues than their sisters, had a shifted acceptance threshold (Reeve, 1989; Liebert & Starks, 2004), and thus they were likely to make more acceptance errors such as failing to attack an alien foundress. An increase in recognition errors was already reported in *Polistes* field colonies usurped by obligate social parasites (Lorenzi, 2003). The difference in tolerance of unrelated individuals is puzzling and requires specific analyses.

With respect to interspecific nest-usurpations, usurpers did not mimic *P. dominulus* host odours. In this case, the data showed that workers from U-nests accepted usurpers as nestmates, but workers from F-nests rejected their sisters' usurpers as strangers. To explain this, we can hypothesize that, when invading *P. dominulus* host-colonies, *P. nimphus* usurpers deposited their odour on the host comb, without changing their epicuticular blend.

It is unreasonable to think that usurpers switched from one strategy to the other according to host-nest species. It is more likely that the different chemical strategies revealed by our experiments arose from different properties of the chemical signature of the two species.

Small quantitative differences exist between wasp colonies of the same species (Bonavita Cougourdan *et al.*, 1991; Lorenzi *et al.*, 1997; Singer, 1998), whereas qualitative differences, although small, exist between the epicuticular blends of *P. nimphus* (Turillazzi *et al.*, 1998) and *P. dominulus* (Bonavita-Cougourdan *et al.*, 1991). The results of the present study showed that *P. nimphus* usurpers changed their own chemical signature and overcame the differences between themselves and host colonies in conspecific usurpations (where only quantitative differences exist). By contrast, they did not mimic host odours in heterospecific usurpations (where qualitative differences exist). There, *P. nimphus* usurpers did not acquire (passively or actively) *P. dominulus*-specific compounds from the hosts: they mimicked only epicuticular chemical profiles similar to their own. However, they stroked their abdomen on host-colonies, which was possibly functional to applying their own odours on host combs.

Obligate social parasites do mimic the chemical signature of host colonies of different species (Dettner & Liepert, 1994; Lenoir *et al.*, 2001; for *Polistes* social parasites: Bagnères *et al.*, 1996; Turillazzi *et al.*, 2000;

Lorenzi *et al.*, 2004) and application of parasites' odours to host colonies seems limited to a few compounds in traces (Sledge *et al.*, 2001; Lorenzi *et al.*, 2004). With respect to obligate social parasites, *P. nimphus* usurpers used a primitive chemical strategy because they mimicked the odours of hosts whose chemical signature was similar to their own but did not acquire a qualitatively different odour. However, when faced with combs of a different species, *P. nimphus* usurpers employed a more brutal chemical strategy, by applying their odours to host combs.

By adjusting their chemical strategy according to the species of host combs, facultative social parasites show that they do not possess the specialized integration strategies demonstrated by their closely related obligate social parasites.

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