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Recognition of a paper wasp social parasite by its host: evidence for a visual signal reducing host aggressiveness

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Obligate social parasite insects are specialized in exploiting the parental service of the workers of another social species by invading their colonies. As social insects are usually aggressive towards intruders, social parasites have to circumvent the host's nestmate recognition system to enter the host colony successfully. Many studies on paper wasps have shown that, after host nest invasion, *Polistes* social parasites change their chemical profile to match the host's odour, thus allowing their acceptance into its colony. However, a social parasite's usurpation strategy may benefit from signals that reduce or eliminate the aggression of the host. We used lure presentation experiments to investigate whether *Polistes sulcifer*, a social parasite of the paper wasp *P. dominulus*, is able to reduce the aggressive reaction of its host. We found that the parasite lure elicited lower host aggressiveness than the conspecific lure, suggesting that parasite species have evolved cues able to inhibit host aggressiveness. We investigated separately the effects of chemical and visual patterns on host aggressiveness. The lower host reaction to the parasite lure was not due to chemical cues, but was elicited by the visual facial pattern of the parasite. Experimental manipulation of this visual pattern demonstrated that the black lower part of the clypeus of the parasite is the trait able to reduce host aggression. This pattern can be considered an honest signal since it visually amplifies the mandibular width, giving information about the parasite's dangerousness.

Obligate social parasite insects have lost the worker caste and the ability to establish nests. Thus, like avian brood parasites, they capitalize on the host's parental care to rear their offspring (Wilson 1971). As social insects are usually aggressive towards intruders, social parasites have to circumvent the hosts to enter the host colony successfully and ensure their reproductive success (Dettner & Liepert 1994; Lenoir et al. 2001; Howard & Blomquist 2005; Lorenzi 2006). Concurrently, the efficient nestmate recognition system of the host has also evolved to minimize the invasion risk, since the potential impact of obligate social parasites on their reproductive success is strong.

Among *Polistes* paper wasps, only three species of interspecific obligate parasites are known, namely *P. atrimandibularis*, *P. sulcifer* and *P. semenowi*, and their parasitic strategies have been well studied (Cervo & Dani 1996; Cervo 2006; Lorenzi 2006). *Polistes* wasps use the blend of hydrocarbons covering the insect cuticle as the principal cue for nestmate recognition (Gamboa 2004) since it is specific for each colony. Studies on the host–social parasite system in *Polistes* wasps show that the parasite species have evolved sophisticated chemical strategies to circumvent the host's recognition systems (Bagnères et al. 1996; Turillazzi et al. 2000; Sledge et al. 2001; Dapporto et al. 2004; Lorenzi et al. 2004). For example, *P. sulcifer*, a social parasite of *P. dominulus*, has a simpler hydrocarbon signature than the host species before usurpation (Turillazzi et al. 2000); however, immediately after usurpation, it starts a process of matching the host's odour and 3 days later its chemical profile becomes very similar to that of the host (Turillazzi et al. 2000). *Polistes sulcifer* females adopt not only the host species' odour but also the colony-specific host's cuticular odour (Sledge et al. 2001). Moreover, during the usurpation period, the parasites (at least two of the three species) have much lower quantities of hydrocarbons than the host individuals (Lorenzi & Bagnères 2002; Lorenzi et al. 2004). This quantitative deficiency could limit the initial aggressive reaction by the host foundresses (Lorenzi & Bagnères 2002), as hypothesized for parasitic ants by Lenoir et al. (2001).

Recent studies (Tibbetts 2002, 2006; Tibbetts & Dale 2004; Tibbetts & Curtis 2007; Tibbetts et al. 2010) have suggested that visual cues could play a role in *Polistes* recognition in addition to the well-known chemical ones. In *P. fuscatus*, the facial and abdominal markings are visual signals of individual identity used by wasps to recognize their nestmates (Tibbetts 2002). Tibbetts

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(2004) suggested that this individual recognition capacity might be widespread in *Polistes*, since eight *Polistes* species show the variability in the markings necessary for individual recognition. Tibbetts & Dale (2004) measured the facial markings of *P. dominulus* females in their new habitat (this species is invading North America, Cervo et al. 2000) and found that large dominant females have a higher percentage of black and a higher 'badge brokenness index' (an indication of the irregularity of the black spots along the clypeus) than smaller ones; the authors suggested that the 'brokenness' is a visual signal of hierarchy level. Brokenness, number and size of the black spots also seem to discriminate between workers and foundresses (Tibbetts 2006). It was recently suggested that this badge of status is a signal of agonistic ability and is important during assessment of rival status (Tibbetts & Lindsay 2008; Tibbetts & Shorter 2009). Cervo et al. (2008) studied the facial markers in natural populations of *P. dominulus*, in their native range; however, they did not find any correlations between facial markers, size and the hierarchical rank of each foundress in its original colony or between facial markers and individual quality of females measured as winter-survival capacity or health status.

Although several studies on chemical and visual recognition ability have been carried out on host species (Dani et al. 1996, 2001; Lorenzi et al. 2004; Tibbetts & Dale 2004; Tibbetts 2006, 2008; Cervo et al. 2008; Tibbetts & Lindsay 2008), no research has focused on the host's ability to recognize a social parasite. The strong impact of a social parasite on the host's reproductive success suggests that the host's ability to discriminate usurping parasites is likely to evolve. The chemical profile of the parasite *P. sulcifer* before nest usurpation is species-specific and is simpler than that of the host foundresses (Turillazzi et al. 2000). Moreover, its facial pattern is dissimilar to that of its host *P. dominulus*: the square head, with often a typical black band in the lower half of the clypeus, makes the parasite's visual cues very different from those of the host (Fig. 1a, b).

As these odour and visual cues are so different between *P. sulcifer* and *P. dominulus*, we investigated the host's ability to recognize

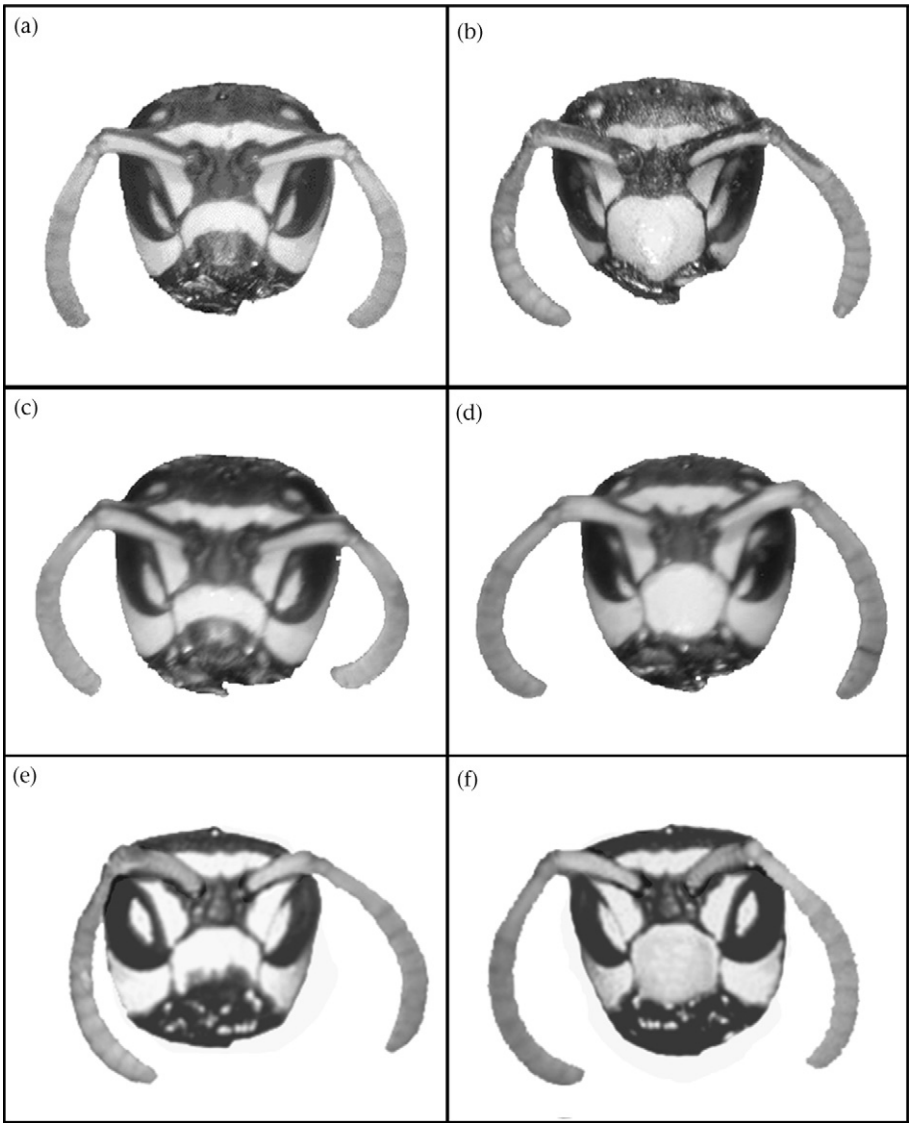

Figure 1. Examples of lures used in visual presentation experiments. (a, b) Original heads of (a) the parasite, *P. sulcifer*, and (b) the host, *P. dominulus*, used in the 'host versus parasite' experiment. (c, d) Parasite heads with (c) yellow paint on the upper half of the clypeus ('unaltered') and (d) completely yellow-painted clypeus ('altered') used as control and experimental lures, respectively, in the 'manipulated parasite' experiment. (e, f) Parasite heads with (e) a typical facial pattern (like lure a) and (f) a natural atypical pattern, with completely yellow clypeus used in the 'unmanipulated parasite' experiment.