Chapter 8
Visual Recognition in Social Wasps

R. Cervo, A. Cini and S. Turillazzi

Abstract Social recognition, i.e. the ability to recognize and assign individual membership to a particular and relevant class, such as caste, dominance status, gender or colony, shapes the amazing organization of insect societies. Traditionally, it has been assumed that social recognition in social insects is mainly governed by chemicals. However, social insects also share information via many other sensory channels, and it has been recently demonstrated that visual signals can mediate several types of social recognition in some species of social wasps. Primitively social wasps, such as paper wasps of *Polistes* genus, are suitable models to investigate visual communication because their combs lack of envelops allowing light to produce visual cues, their colonies are small, they have a good vision, they show a remarkable individual within-colony colour variation and, finally, they show an intense social life based on social recognition. In this chapter we reviewed the role of visual cues in social recognition inside and outside social wasp colonies focusing both on the intraspecific and interspecific recognition contexts.

Introduction

Recognition ability is an essential requirement for social behavior. Social insect colonies are well integrated societies characterized by a high level of cooperation among colony members (Wilson 1971). Such complex social interactions

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are possible thanks to the continuous exchange of information among individuals. Indeed, all forms of response following social interactions depend on some types of recognition. For example, the ability to discriminate nestmates from non-nestmates allows each colony member to favor the self and at the same time to repel the non-self, thus making social insect colonies highly defended xenophobic fortresses (Van Zweden and d'Ettorre 2010). The amazing organization of a social insect colony is however based not only on nestmate recognition but more in general on the ability to recognize and assign individual membership to a particular and relevant class, such as caste, dominance status, gender and so on.

In many social insects, the combination of a high number of individuals per colony and the common tendency to nest in sheltered and dark places (e.g. soil or enveloped nests) has favored the evolution of a large repertoire of chemicals (pheromones) to mediate intra-colonial transfer of information. Traditionally, it has been assumed that social insect life is governed by chemicals (Howard and Blomquist 2005; see this book) although social insects can transfer information to their nestmates, conspecifics and heterospecifics also via many other different channels, including the acoustic (reviewed in Kirchener 1997), vibrational (reviewed in Hunt and Richard 2013) and visual one (e.g. Nieh 2004). However, since a few time ago, the cues involved in social recognition in bees, ants, termites and wasps have been believed to be almost exclusively the chemical ones, with the hydrocarbons that cover the insect cuticle playing a major role (Howard and Blomquist 2005; see this book).

Already one century ago Wilhelmine Enteman (quoted by Strassmann 2004) described the amazing colour variation within the members of a *Polistes* wasp colony, but only recently this variability suggested that also visual signals can be strongly involved in mediating several types of social recognition (Tibbetts 2002; Tibbetts and Dale 2004).

In this review we will discuss the influence of visual cues in social recognition in primitively social wasps that represent interesting models to investigate the functioning and evolution of visual recognition. Indeed, these societies are rather small, with poorly differentiated phenotypes and highly flexible (almost all individuals can become fertile and reproduce). More than simply aiding researchers in their experimental work, these features represent a favourable environment where a full range of different recognition systems can evolve, from individual recognition (IR) to status recognition. Moreover, contrary to many social insects that live in the darkness (underground as many ants or termites, or in enveloped nests such as bees and some more eusocial Vespinae), primitively social wasps such as *Polistes* and most Stenogastrinae live in open nests, where communication by using reflected light to produce visual signals is possible.

This review will focus on *Polistes* paper wasps, as the bulk of visual recognition studies (more than the 95 %) has been carried out in this genus. Nonetheless, we will discuss also available information on Stenogastrinae hover wasps, which recently raised attention as they can provide independent test on the evolution of visual recognition in a different social clade (Baracchi et al. 2013). The review will cover the importance of visual cues in mediating social recognition inside and outside social insect colonies, both in the intraspecific and interspecific context.

Status Recognition and Quality Signals

A paper published by Tibbetts and Dale on *Nature* magazine in November 2004 revolutionized what previously thought about the communication system in *Polistes* paper wasps. Basically, this study showed that differences in the black area on the yellow clypeus of female *Polistes dominula* make a variable facial pattern that conveys information about the competitive ability of an individual to potential opponents.

These conventional signals, also known as ‘badges of status’ (Smith and Harper 2003), have been largely studied in passerine birds (Rohwer 1975, 1977; Senar and Camerino 1998) and lizards (Whiting et al. 2003), where small patches of color on the body of each individual influence the outcome of contests over resources in a group. These signals, that are claimed to be the animal equivalent of sergeants’ strips (Roper 1986), allow to reduce costs and injuries linked to overt fights (Smith and Harper 2003). Badges of status are generally considered to be ‘conventional’ signals as they are not causally linked to resource-holding potential and they have no production cost (Smith and Harper 1988). However, being cost free, they could be exploited by low quality individuals to cheat about their real quality. Theory predicts that social costs guarantee the honesty of ‘badge of status’ signals because the cheater benefits should be overwhelmed by increasing challenge by group mates (see Smith and Harper 1988).

In *Polistes* paper wasps contests typically occur in early Spring when inseminated females (foundresses) exit from their overwintering refuges and search for a place where start a new colony. In *P. dominula,* a model species for sociobiological studies (Starks et al. 2006), nest can be founded either by a single foundress or by a group of associate foundresses (Pardi 1948). Before nest foundation, foundresses typically engage in harsh fights to determine the rank position of each individual within a group. After this early period, aggression decreases and ritualized non-aggressive dominance interactions among co-foundresses on the nest determine a linear hierarchy (Pardi 1948). The dominance order mirrors the reproductive skew in the colony: the dominant foundress monopolizes reproduction and becomes the principal egg layer (more than 90 % of the eggs in a *P. dominula* nest belongs to the alpha female, Queller et al. 2000) while the subordinate foundresses, although potentially capable to reproduce, renounce to their direct fitness and engage in typically worker tasks as foraging, nest building, colony defense and brood care (Pardi 1948).

The potential conflict over nest ownership and reproduction among co-foundresses may have represented strong selective pressures driving the evolution of badge of status signals. Given their high variability, the markers on wasp faces may indeed represent good candidates, allowing individuals to quickly assess the agonistic abilities of potential rivals and minimizing the time and costs during the nest founding stage contests. Indeed, facial pattern variability of foundresses of *P. dominula* is remarkable, especially in some areas, such as in North America (where the species has been recently introduced from its native Eurasian range; Cervo et al. 2000; Liebert et al. 2006). The yellow clypeus can have one or more black spots or no black spots at all, and the size and the shape of the spots can be very variable (Fig. 8.1). In order to catch and quantify this variability, Tibbetts and Dale (2004) introduced a new index, called 'badge brokenness index', that represents a measure of pattern disruption (by calculating the standard deviation of amount of black pigment deposited along the horizontal gradient located between the two peaks).

If facial markers are badges of status, they should be linked to some individual quality feature (such as body size) and to social dominance. Indeed,

Species	**Areas and parameters investigated**
P. dominula	Area, shape, presence of black pigmented spots on the clypeus; Size and shape of the abdominal spot
P. fuscatus	Pattern of facial markings: eye stripes, eyebrows, clypeus pattern, abdominal stripes
P. exclamans	Width, lenght and area ofthe brown stripe on the clypeus
P.metricus	Pattern of facial markings: eye stripes, eyebrows,clypeus pattern, abdominal stripes
P. satan	Percentage of the black/brown painted area relative to the head area
P. sulcifer,	Presence/position of the black band on the clypeus
P. semenowi	Presence/position of the black band on the clypeus
L. flavolineata	Size of the brown pigmented area on the face
L. vechti	Size of the brown pigmented area on the face
P. melly	Number of white stripes on the abdominal tergites

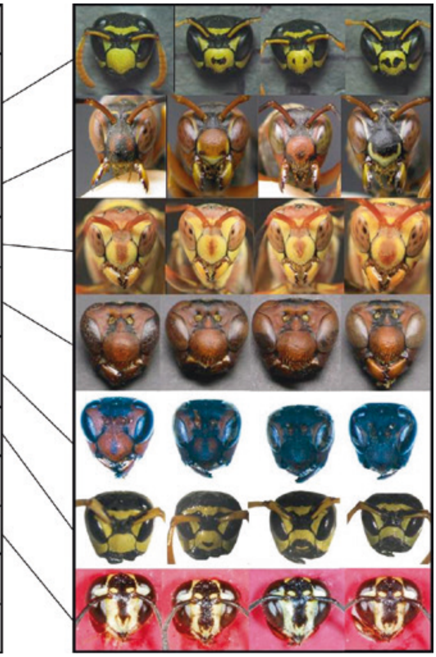

Fig. 8.1 Variability in facial patterns in some *Polistes* and Stenogastrinae wasps and the areas investigated in each species. From *top* to *bottom*: *P. dominula, P. fuscatus*, *P. metricus*, *P. exclamans*, *P. satan*, *P. sulcifer*, *L. flavolineata*; photos of facial patterns of *P. semenowi*, *L. vectti* and *P. melly* are not shown. Photo credits E.A. Tibbetts (*P. fuscatus*, *P. exclamans*, *P. metricus*), F.S. Nascimento (*P. satan*), D. Baracchi (*L. flavolineata*)

brokenness index (as well as the number of spots and the percentage of clypeus black) positively correlated with body size and facial markers predicts social rank in laboratory dominance trials (Tibbetts and Dale 2004). Unfamiliar pre-founding females with different facial pattern collected in the new invaded area of this species (Ithaca, New York) were paired for body size and their interactions where observed for two hours in an experimental arena: mean badge brokenness as well as number of spots (but not percentage of clypeus black) were slightly (see Strassmann 2004) higher in females that were dominant in the contest trials than in subordinate females. Moreover, the mount rate performed by alphas on betas, to reinforce their position in each pair after dominance was established, was positively correlated with the facial pattern of betas, indicating that subordinate foundresses received more aggression if they had badges associate with higher dominance (Tibbetts and Dale 2004). Finally, experimentally alterations of the badge of subordinate individuals, after hierarchy was established, by painting with a mark indicating a higher status than their real one (simulating cheaters) made them be punished by alphas. Overall, the results obtained by Tibbetts and Dale (2004) suggest that facial markers are signals of quality and that low rank individuals are prevented to cheat about their status, even though its signaling would appear to be cost free, by the social costs they would pay. In this way, honesty should be maintained as cheating subordinates would be punished. As pointed out by Strassmann (2004), it is surprising that no effects on behavior were observed when facial markers manipulation was performed before the establishment of the dominance order because by painting a female face with a higher status mark she should have had more chances to become dominant. However, the response to signals of agonistic ability are often reported to be context dependent also in birds; which may explain why sometimes wasp females with experimentally increased badges do not increase their social rank.

An expected consequence of the “badge of status hypothesis” is that the facial patterns of co-foundresses in wild associative foundations would predict the dominance order, i.e. dominant individuals would have more black spots and more ‘broken’ facial pattern than subordinate individuals. Surprisingly, Cervo et al. (2008) didn’t find any correlation between rank position and facial pattern (considering the number of spots, the percentage of black area and the brokenness index) by checking the visual markers of foundresses in wild spring foundations observed for dominance hierarchies in several Italian populations, i.e. in the native range of the species. Similar results were reported for an another native population of *P. dominula* in Spain (Zanette and Field 2009; Green et al. 2012). Such differences could be due to the low frequency of females with clypeus marks in the European studied populations in comparison with American one (Tibbetts and Dale 2004; Cervo et al. 2008; Zanette and Field 2009). This strictly geographic variation in signaling among different populations of this species (Tibbetts et al. 2011a, b; Green et al. 2012) suggests a possible association between facial pattern and climate. Wasps inhabiting cooler areas show more spotted and broken facial patterns than those living in warmer areas (Tibbetts et al. 2011a, b; Green et al.

2012). Moreover, Green et al. (2012) experimentally showed that wasps reared during the pupal stage in cooler conditions had higher brokenness than their nestmates reared in warmer conditions. Basically, variation in melanin pattern can play a role for efficient thermoregulation in different thermal conditions, by permitting more rapid body heating (Green et al. 2012). But, as underlined by Tibbetts and Dale (2004), the amount of melanin on the clypeus represents less of 1 % of the total amount of the pigment on the body surface and it is not known if wasps with more black clypeus show also greater body melanisation, The abundance of wasps with entirely yellow clypeus in South Europe populations (Spain and Italy) may thus locally limit the evolution of visual social recognition (Green et al. 2012) thus explaining the contrasting results obtained by studies carried out on populations of different climatic areas.

A badge of status is expected to be a reliable signal of quality and its honesty (association between true quality and signaling) is maintained and enforced by social costs (Smith and Harper 2003). As expected, in the American population of *P. dominula* studied by Tibbetts and Dale (2004), all indicators of status badge (number of spots, percentage of clypeus pigmented black and brokenness index) were correlated with body size of foudresses (measured as head width) that is a good predictor of dominance (even if no absolute, see Cervo et al. 2008), suggesting that clypeus marks represent reliable indicator of quality. Moreover, facial brokenness was also found to be linked to titers of Juvenile Hormone, a hormone involved in agonistic a interactions (Tibbetts et al. 2011a, b). Support for the importance of facial pattern as quality signal comes also from the study of the signal developmental properties. While having an heritable component, the quality signal is highly influenced by environmental factors during larval and pupal life. In addition to the importance of temperature (Green et al. 2012), food supplementation experiments showed that rearing conditions influence quality signal development in American population (Tibbetts and Curtis 2007). Wasp larvae reared with supplemental food develop facial patterns advertising higher agonistic quality (i.e. higher brokeness) than larvae reared without supplement, supporting the idea that black marks convey information of quality linked to early nutrition. These findings could also account for the different facial pattern in *Polistes* “castes” (Tibbetts 2006a; Tibbetts et al. 2011b): workers, which experience reduced larval nutrition compared to foundresses (Toth et al. 2009), show lower facial pattern brokenness.

Other species of wasps showing variable clypeus pigmentation patterns have been tested to assess whether variable facial pattern function as a conventional signal of agonistic ability. Three species of *Polistes* paper wasps, *P. satan* (Tannure-Nascimento et al. 2008), *P. exclamans* (Tibbetts and Sheehan 2011), *P. gallicus* (Petrocelli et al. 2014) and a stenogastrine wasp, *Liostenogaster vechti* (Baracchi et al. 2013) showed visual markers that convey information on agonistic ability.

However, different studies have used different indicators of quality in addition to body size. Reproductive status (measured as ovarian development) was found to be linked to variation of visual signals both in the stenogastrine wasp *L. vechti* (Baracchi et al. 2013) and in *P. satan* (Tannure-Nascimento et al. 2008), being the wasps with more developed ovaries (i.e. dominant individuals) those with more dark facial markings.

Contrary to what was expected, nor correlation between facial pattern parameters and foudresses body size (and body weight), (Cervo et al. 2008; Zanette and Field 2009; Green et al. 2012), neither correlation between facial pattern and both probability of surviving winter and health status (Cervo et al. 2008) were found in European populations of the species, confirming that clypeus pattern doesn't mirror the true quality of bearer in wasps belonging to such populations (but see Tibbetts et al. 2011a, b for contrasting results).

Although all these studies provide correlational evidences for facial pattern as quality signal, a simple test to evaluate the assessment of conspecifics via visual clypeus markers during foraging contexts has furnished an experimental support for facial markers as quality signal in *P. dominula* (Tibbetts and Lindsay 2008). Wasps were tested in choice trials to evaluate their preference for food patches guarded by conspecifics with different facial pattern; they showed to perform their choice on the basis of the guard facial pattern by avoiding to eat food patches controlled by guards with facial patterns indicating a high quality level. Moreover, Tibbetts (2008) provided evidences that the tested wasp responses to guard badge are context dependent. However, when the test was repeated in a native European population (Spain, Green and Field 2011a) no evidences that wasps use facial pattern to assess rival quality were found, confirming again no communicative role of clypeus marks in European populations. More recently, another study (Branconi et al. in prep.), tested for a signal function of the clypeal pattern by presenting wasp lures with different facial patterns to colonies of another native population (Italy) and showed that clypeal patterns are not involved in rival assessment in a competitive context (colony defense).

Finally, facultative intraspecific parasitism—i.e. nest usurpation by a conspecific female- is another context (Cervo and Dani 1996; Cervo 2006) where information born on facial pattern could be used by colony owners to assess the fight ability of potential rivals. Tibbetts and Shorter (2009) showed that the outcome of the context in *P. dominula*—conflict *versus* cooperation—is influenced by both facial pattern an body size. Challenger with more facial markers than the nest owner has more probability to usurp the colony that challenger with fewer markers than owner. An analogous result has been found in the European species *Polistes gallicus* (Petrocelli et al. 2014): queens of this solitary founding species usually experience a high rate of intraspecific usurpation (Dani and Cervo 1992) and they use visual black mark on the clypeus of the potential usurper to assess the opponent fighting ability (Petrocelli et al. 2014) and modulate their response. Moreover, Tibbetts and Injaian (2013) found that foundresses of *P. dominula* preferentially associate with other foundresses that have similar facial pattern. This tendency may increase the likelihood to form associations among related individuals as wasps from the same nest have more similar facial patterns (Tibbetts 2006a, b; Tibbetts et al. 2010). As a result, co-foundresses associations in wild colonies could be influenced by facial pattern similarity (Tibbetts and Injaian 2013) in addition to the well-known role of chemical signature similarity (Dapporto et al. 2004), even if stable and free-conflict cooperation would be based on a differential facial pattern hierarchy (Tibbetts and Dale 2004).

Overall, the growing literature on this topic suggest facial pattern could work as badge of status in some populations (e.g. North America) but not in other (e.g. Spain and Italy). It is possible that these contrasting results could be partially due to the different parameters used to evaluate (i) the variation in facial pattern (the sheer number of spots, the percentage of black area on the clypeus or the more complex brokenness index), (ii) the individual quality (size, weigh, ovarian development, health status), and (iii) the measures of dominance in the different studies. For example, it could be important to confirm the goodness of plastic arena experiment carried out for two hours as generalization of what happens into the wild because, in nature, the establishment of the dominance hierarchy requires often long time and sometimes it can change with the time. Returning to the field to verify the results obtained in captivity is thus fundamental. For example, the comparison of quality signals between gynes (future foundresses) and queens (top rank foundresses) suggests that brokeness is indeed not strongly associated with reproductive success. As not all gynes will survive winter until the founding phase and become queens on their nest (as they may be subordinate foundresses of low social rank, not having reproductive benefits) we can predict successful queens to have higher quality signals than gynes. Contrarily, Tibbetts et al. (2011a, b), investigated several populations along a latitudinal gradient in Europe and North America and found that gynes and queens have similar facial patterns (Cervo et al. 2008; Tibbetts et al. 2011a, b). As a confirmation, the only studies carried out so far on *Polistes* to evaluate the importance of facial patterns in wild population failed to find any adaptive value associated with facial patterns (Cervo et al. 2008; Green and Field 2011a). A similar investigation in the American population will reveal the importance that facial patterns play in *P. dominula* in the wild and it is thus strongly needed to conclusively evaluate the importance of facial patterns in the population where most positive evidence have been collected (Green and Field 2011a).

Individual and Familiar Recognition

The most accurate form of social recognition is IR, i.e. the ability to recognize individuals according to their distinctive features (Halpin 1980, Dale et al. 2001, Wiley 2013). This ability can convey relevant benefits to social animals, both in competitive and cooperative interactions. Whenever there are repeated interactions among multiple individuals with differing features and states, IR may allow to modulate social behaviour according to prior experience with specific individuals. For example, when scrambling for a limited resource, opponents may benefit by avoiding repetition of costly fights by individually recognizing specific high quality opponents (Tibbetts and Dale 2007). Thanks to its benefits (despite some costs, in particular the lower possibility to cheat when having easily recognizable distinctiveness, see Tibbetts and Dale 2007) IR recognition is now considered to be widespread both in vertebrates and invertebrates (reviewed in Gherardi et al. 2012 for invertebrates, Halpin 1980 and Tibbetts and Dale 2007 for vertebrates).

Insect societies are not usually considered as harbouring IR abilities, being thus often represented as impersonal societies lacking specific individual bonds (Wilson 1971). Indeed, the usually large size of the colony and the short life of its members may prevent the evolution of IR and promote, on the contrary, other kind of social recognition such as familiar and nestmate recognition. Not all insect societies however reach the highest peaks of complexity and crowdedness. In many genera of primitively eusocial species, such as Polistinae and Stenogastrinae, societies are formed, for a large (or even the entire) part of their colony cycle, by just few to dozens individuals (Reeve 1991; Turillazzi 2012). These societies are usually characterized by intense direct conflict over access to reproduction, which are regulated by complex yet stable social interactions (Bourke 1999). Being able to recognizing who's who and behave appropriately may thus reveal to be crucial.

Recently, a case of IR have been suggested (Tibbetts 2002) to exists in a temperate paper wasp species from North America, *Polistes fuscatus*, which has some crucial features that qualifies it as potentially harbouring IR: (1) small group size and (2) repeated social interactions that (3) dramatically affect individual fitness payoffs among (4) individuals with highly variable distinctiveness.

Similarly to *P. dominula, P. fuscatus* colonies are usually founded by multiple foundresses in Spring and a linear hierarchy is soon established. *P. fuscatus* females have a very large phenotypic variability in their yellow facial and abdominal markings, which may be present or absent and vary in width and length (Fig. 8.1, Tibbetts 2002).

Tibbetts (2002) demonstrated that the presence of these markings allow wasps to recognize individuals with which they previously interacted (e.g. nestmates). When a wasp was returned to the nest after an experimental manipulation of her facial or abdominal markings with paint, she received more aggressions from nestmates than a control wasp (painted in a way that did not alter their markings) (Tibbetts 2002). As predicted for actual identity signals (Dale et al. 2001), *P. fuscatus* facial and abdominal markings are not condition dependent as they are not associated with wasp size or dominance rank, (Tibbetts 2002) nor with wasp pre-emergence rearing conditions (Tibbetts and Curtis 2007).

This recognition ability is achieved learning the yellow-black patterns of the wasp, as proved by the fact that aggression toward nestmates with altered markings declines over time, as these novel marking configuration becomes familiar to nestmates (Tibbetts 2002). Indeed, *Polistes fuscatus* wasps seem to be specialized in face learning. Through a conditioning protocol Sheehan and Tibbetts (2011) were able to show that *P. fuscatus* are more skilled at learning to recognize wasp faces than non face images or manipulated faces (such as re-arranged or antennaeless faces).

The markings configuration learned in social encounters is then stored in wasp brain and wasps are able to retain this information up to one week after, even if multiple social interactions with many other wasps occur during this period (Sheehan and Tibbetts 2008). Such long term memory may be stabilized via protein synthesis, as occur in long term olfactory memory in ants (Guerrieri et al. 2011).

The experiment discussed above showed that female *P. fuscatus* use facial and abdominal markings to recognize individuals with whom they have previously interacted or seen. According to Tibbetts and Dale (2007) this ability can be classified as IR and, indeed, the same experimental approach has been used to assign IR abilities in many species of invertebrates and vertebrates (Tibbetts and Dale 2007; Gherardi et al. 2012). However, disentangling IR from other form of class level recognition (such as familiar recognition) is not an easy task (Tibbetts and Dale 2007; Gherardi et al. 2012; Wiley 2013). Indeed, the IR definition itself has been debated (Tibbetts and Dale 2007; Steiger and Muller 2008; Tibbetts et al. 2008) and the extent to which invertebrate species are able of IR still remain uncertain (Thom and Hurst 2000; Gherardi et al. 2012; Wiley 2013). A key feature of IR process is that it requires individuals to “uniquely identify each social partner” (Becher 1989; Lai et al. 2005; Tibbetts and Dale 2007), i.e. each individual should be treated in a specific way according to the significance it has to the subject. The largest part of studies on IR has unfortunately the shortcoming of not allowing to separate familiar recognition from true IR (Lai et al. 2005; Gherardi et al. 2012; Wiley 2013). Indeed, the first occurs when individuals discriminate between familiar and unfamiliar conspecifics, i.e. previously met or not met individuals, by showing for example reduced aggression or reduced interest in known partners. This recognition is indeed a class-level recognition, in which individuals are categorized in two classes (met or not previously met, unknown) and it is very widespread in invertebrates (Gherardi et al. 2012). True individual recognition (TIR) is, on the contrary, the ability to discriminate among individuals, who may share several features (such as familiarity, dominance rank, gender), on the basis of a specific configuration of their features (e.g. appearance, odour, behaviour), (Gherardi et al. 2012; Wiley 2013). From an operational point of view it should be tested by evaluating if individuals show different responses to equally familiar individuals with differing significance to the subject (Lai et al. 2005). Currently, no specific experiments to test this possibility have been undertaken in social wasps (Wiley 2013). The most parsimonious hypothesis is thus that social wasps show familiar recognition thanks to the use of visual cues.

The ability to perform familiar recognition on the basis of visual cues could be indeed quite widespread in social wasps. As far as there is enough variability in markings to allow for distinctiveness among a certain number of frequently encountered partners (such as nestmates in small insect societies) and the rest of unknown/unfamiliar conspecific individuals (which seems to be the case for many *Polistes* and stenogastrine wasps), the ability to learn specific configuration of facial/abdominal marking should not be out of the possibility of social wasps. Indeed, the finding that familiar recognition based on visual cues also occurs in a hover wasp (*L. flavolineata*, Baracchi et al. 2013) suggests the intriguing hypothesis that this ability may be quite common in social wasps.

Visual Recognition and Sex

Generally, in Hymenoptera, male-male competition for mate and mate choice occur far from the nest. In such a context, an information exchange between male and female is required to recognize species, sex, sexual maturity and to attract and find each other. In social wasps, males typically have lek- or swarm-based mating systems (see Turillazzi and Cervo 1982; Beani et al.1992; Beani 1996; Turillazzi 2012; Batra 1980; Spiewok et al. 2006). Males typically patrol non resource sites at species-specific time of the season and/or hours of the day. Male performances usually occur at traditional landmarks that differ for location among sympatric species. Conspicuous aggregation of mature males at species-specific timing and landmarks visually attract conspecific females facilitating successful outbreeding.

However, male fitness is limited by the availability of females visiting males aggregations and males vigorously compete at leks or at swarms to gain access to females. On the other hand females have a wide choice of males and gain in fitness by recognizing high quality males. This results in skewing reproduction among males and in selecting male ornaments to minimize competition costs and address female choice (Andersson and Simmons 2006).

Males of some species of social wasps are reported to use visual signals that allow recognition of strength ability during intra-sexual conspecific competition and, at the same time, of male quality to address the female choice.

Males of several species of stenogastrine wasps exhibit a visual display during their patrolling behavior in shady wet tropical forest (for a review see Turillazzi 2012). During their aerial displays, males of *Parischnogaster* wasps, by extending their abdomens, show large white stripes on the dorsal anterior part of the gasters that are conspicuous visual spots against the dark background of the forest. These strips become invisible when males don’t stretch their abdomen during patrolling flights or are in resting position. Moreover, the white stripes are a sexual dimorphic trait as they lack in females. These stripes described for the first time by Padgen (1962) for *Metischnogaster cilipennis*, *M. drewseni* and *Parishnogaster striatula*, have been reported more recently for other species, such as *Parishnogaster mellyi* and *P. nigricans serrei* (Turillazzi 2012). Male of *P. mellyi* usually perform a zig-zag display after the prolonged stripes display (Beani and Turillazzi 1994). The duration and the frequency of this performance are positively correlated both with the outcome of aerial duels and the permanence on the patrolling spots until the arrival of the females which occurs towards the end of the patrolling period; this suggests that this male trait may give information to recognize both male strength and quality (Beani and Turillazzi 1999). Experimental manipulation of white stripes in a captivity study on *P. mellyi* males (Beani and Turillazzi 1999) demonstrated the function of this visual ornament as badge of status (Berglund et al. 1996): the addition of one white stripe on the abdomen of male elicits more inspections/aggressions by competitors and more explorations by flying females (Beani and Turillazzi 1999). Interesting, artificially white-painted males showed to be unable to support the social cost induced by the alteration of their badges: they shortened the period and the frequency of their visual display and performed very frequently feeding stops during their performance. This suggests that the visual white-stripes exhibition has costs for the patrolling males and only individuals of good quality resist at prolonged visual display.

Analogously, two recent papers on *P. dominula* (Izzo and Tibbetts 2012) and *P. simillimus* (De Souza et al. 2014) suggested that sexually selected visual signals could be important in males of *Polistes* paper wasps too. In *P. dominula* visual signals of males may be represented by dorsal yellow spots placed on the first abdominal segment. Similar spots are present on females too but they lack the variation which characterizes males dorsal spots. According to Izzo and Tibbetts (2012), the sexually dimorphism and the variation in both size and shape of male dorsal spots make them excellent candidates as recognition signals in both intra- and intersexual selection. In *Polistes* wasps, males aggregate at traditional landmarks (Beani and Turillazzi 1988; Beani et al. 1992; Beani 1996), where each male vigorously defends little territory against other males. This lek-based mating system allows females to make their mating choices by sporadically visiting such areas where males gather and maintain their leks. Laboratory experiments carried out by Izzo and Tibbetts (2012) showed that *P. dominula* males with smaller and elliptically shaped spots were more dominant over other males, were often the winners during the male-male contests and were more preferred by females. Once again manipulation of male spots shape and size showed that the morphology of yellow spots works as quality signal driving the outcome of both intra- and inter-sexual interactions. According to Izzo and Tibbetts (2012) an unexpected data regards the lack of relationships between male dominance and female choice as generally it is assumed that female preference is based on male rank position, suggesting that in this species female choice probably is not simply based on male rank (Izzo and Tibbetts 2012). Similar to *P. dominula*, also *P. simillimus* show sexual dimorphism and variation in size and shape of male head pigmentation and abdominal spots, both of which seem to influence females mating choice (De Souza et al. 2014). However, it should be considered that male dominance data were obtained in both cases in artificial context very different from what happens in the wild (and indeed, for *P. simillimus*, male behavior in the field is not known, De Souza et al. 2014). In the field, *P. dominula* males defend their territories by engaging very strong competitions with neighboring males but no dominance contexts (with bites, mounts and submissive behavior) are observed (Beani 1996). It is possible that other parameters of male performance not obviously considered in a laboratory study (such as territory size and its localization in the lekking area or/and the male flight activity at the lek) may be the basis of *P. dominula* female choice. Although the laboratory results on visual ornaments of *P. dominula* and *P. simillimus* males are intriguing, future studies carried out in the wild will be fundamental to better understand the role of visual recognition signals at leks, as pointed out by Izzo and Tibbetts (2012).

Visual Signalling Between Species

The researches discussed so far suggested that visual cues play a relevant role in social recognition between conspecific individuals, in particular shaping intraspecific aggressive interactions. Conflicts, however, may also occur among species and competition between sympatric species may be associated with the access to limited resources such as food or nesting sites (e.g. *P. dominula* and *P. nimpha* in southern Europe, Lorenzi and Caprio 2000, or *P. dominula* and *P. fuscatus* in North America, Gamboa et al. 2002), and with nest usurpation (Cervo and Dani 1996; Cervo et al. 2004; Cervo 2006).

The large variability in *Polistes* facial markings (at both the intra and interspecific level), together with their use in intraspecific communication in several species, opens the possibility that visual cues play a role also in interactions between species.

An outstanding model to evaluate the importance of visual signalling in interspecific contests is represented by *Polistes* social parasites and their hosts. Social parasites exploit the host parental cares in order to rear their own brood, saving the costs of building the nest, foraging and taking caring of the brood (Wilson 1971). Inside *Polistes*, obligate social parasitism—i.e. species lacking the worker caste and unable to found colonies on their own—occurs in three monophyletic species: *Polistes sulcifer*, *P. semenowi* and *P. atrimandibularis* (Cervo and Dani 1996; Cervo 2006; Choudary et al. 1994; but see Buck et al. 2012 for the possible existence of other parasitic species in north America). Parasitism is the only reproductive option for *Polistes* obligate social parasites as they must completely rely on the host worker brood care to rear their own reproductives (Cervo 2006). Parasitism imposes dramatic costs to the host colony, which usually is not able to produce reproductives (Cervo 2006, but see Cini et al. 2014 for evidence of workers rebellion).

The diametrically opposed interests of social parasites and hosts, represented strong selective pressures that led to the evolution of several morphological, physiological and behavioural adaptations in both species (Cervo 1994, 2006; Lorenzi 2006; Ortolani et al. 2008; Ortolani and Cervo 2009, 2010; Petrocelli and Turillazzi 2013). In particular, social parasites evolved sophisticated sensory deception mechanisms to break host's barriers by exploiting their communication systems (Lorenzi 2006). At the same time, hosts may benefit from developing their recognition system and tuning their visual abilities toward the recognition of parasites and the assessment of their strength.

Visual cues could be involved in host-parasite interactions in two main ways. On one hand, hosts may be selected to recognize the "possible" differences in parasite appearance to readily recognize parasites and adopt the best possible strategies to counteract them. On the other hand, parasites may be selected to exploit host visual recognition system to deceive the host. As far as the host recognition system depends on visual cues, it would be advantageous for the parasite to evolve specific adaptations to visually trick the host.

Recently, a possible case of the involvement of visual cues in between-species interaction has been suggested to exist in the social parasite–host system *P. sulcifer–P. dominula*. *P. sulcifer* has conspicuous black patterning on the clypeus, which consists in a black band which is usually contiguous to the black mandibles, forming a continuous large black area in the lower part of the face (Ortolani et al. 2010), (Fig. 8.1). Behavioural bioassays with lures presentation (heads of dead wasps with different facial patterns) showed that the peculiar parasite facial pattern reduces host aggressiveness: host foundresses were more aggressive toward conspecific heads than toward parasite heads (Ortolani et al. 2010). Experimental pattern manipulation revealed in addition that the black lower part of the parasite clypeus (hereafter band) is the trait responsible for this reduction in aggressive responses, as parasites with artificially removed black band were more attacked than control parasites (Ortolani et al. 2010).

The first, most logical explanation is that parasites reduce host aggressiveness as their facial pattern signals a high status and good fighting abilities. This could occur by 'tricking' host foundresses by using host signalling system.

As discussed above, clypeal patterns in the host species are suggested to function as status signals (or 'badges') that indicate the resource holding potential of the bearer (Tibbetts and Dale 2004), so that foundresses modulate their aggressiveness toward unfamiliar opponents on the basis of their visual appearance (Tibbetts and Dale 2004; Tibbetts and Lindsay 2008; Tibbetts et al. 2010). The clypeal patterns of the parasite may thus similarly function as signals of status, conveying the information of a high quality and highly dangerous bearer, finally decreasing host foundress's aggressiveness (Ortolani et al. 2010, Green and Field 2011b for *P. semenowi*). Alternatively, parasites may have evolved an independent quality signaling system, in which different facial pattern honestly mirror individual quality (e.g. fighting ability), and host foundress may thus evaluate opponents fighting abilities upon their facial patterns. Some considerations seem however to argument against both hypotheses. First, the link between opponents facial patterns and aggressive responses has not been confirmed in the native range of *P. dominula*, where parasite-host interaction takes place (Green and Field 2011b; Branconi et al. in prep). Moreover, the parasite pattern is not exactly the same as the host one: the black area is relevantly larger, it extends down to the mandibles and melanin is more uniformly distributed across the clypeus, thus largely reducing pattern disruption (Ortolani et al. 2010; Green and Field 2011b). Finally, parasite facial pattern is not related to any fighting ability parameter taken into account so far (Cini et al. 2015).

An alternative hypothesis is that the reduction in host aggressiveness toward parasites may occur because the black band amplifies the width of the mandibles, which represent the primary weapon used during fight between *Polistes* wasps (Cervo 2006). Indeed, in the host species, mandibles are black and surrounded by yellow facial areas, so that host foundresses may estimate mandibular size of the opponents (and thus their fighting ability) by evaluating the size of the black area in the lower part of the head. When faced to a parasite head, foundresses would overestimate its mandibular size, thus reducing their aggressiveness to avoid fatal injuries (Ortolani et al. 2010). Ortolani et al. (2010) considered the black band attached to the mandibles as a signal that visually amplifies the mandibular width, thus giving information about the parasite's dangerousness.

This hypothesis did not receive support from recent experiments (Cini et al. 2015). A key assumption is that parasites may benefit from amplifying their mandibular size only if hosts use this cue during intraspecific encounters, that is to say if host aggression toward conspecific intruders depends, among many factors, also on their mandibular size. However, no difference was observed in the aggressive response of *P. dominula* foundresses toward conspecific head lures with mandibles size artificially manipulated with paint (increased or decreased) suggesting that the host species females do not rely on opponents mandible size to modulate their aggression (Cini et al. 2015). This makes rather unlikely that parasites evolved a visual cheating strategy based on the amplification of a cue not taken into account by the host they must cheat.

The likelihood that facial pattern evolved as sensory deception strategy by the parasite is also made less likely by the null fitness benefits associated to a particular clypeal patterning (Cini et al. 2011; Green and Field 2011b). Laboratory studies which used real usurpation demonstrated that clypeal patterning has a null role in determining the outcome of usurpation contests: parasites with different facial patterns had no different chances of winning a contest with the host (Cini et al. 2011; Green and Field 2011b). On the contrary, head size was the only determinant predictor of the likelihood of winning an usurpation contest (Cini et al. 2011; Green and Field 2011b).

Turning the attention to the host ecology may help to find an explanation. While parasitisation represents a very dangerous event for *P. dominula*, also conspecific individuals represent a major threat. Indeed, nest usurpation by foundresses from other nests is very common in this species, likely due to nest failure or predation (Cervo unpublished data). Despite obligate parasite prevalence could be locally very high (up to 50 % of nests are parasitized in some populations, Ortolani and Cervo 2010), the largest part of *P. dominula* populations experience a null or low parasitic pressure, as parasites are restricted to host populations near mountains, were parasites overwinter (Cervo 2006). Moreover, we could expect intraspecific parasitism pressure to be even higher in parasitized populations, where foundresses displaced by the parasites will try to usurp other conspecific nests. Overall, we may suppose that intraspecific parasitism could be a more common threat for *P. dominula* foundresses. So, a possibility to explain the lower aggressiveness toward parasites head is thus that for *P. dominula* foundresses a conspecific intruder may represent a bigger threat than a parasite. Consequently, host foundresses would thus react more aggressively toward conspecific intruders than parasites. Indeed, lure presentation experiments showed that when the parasite facial pattern is altered by displacing the black band in the middle of the clypeus, thus mimicking a host-like facial pattern, host aggression increases (Cini et al. 2015).

Evolution of Visual Recognition Abilities and Conclusive Remarks

The main pressures that shape social life selected for the evolution of a full range of recognition systems in primitive insect societies. The paradigm that social insects live in a world of smell and that their social life is governed by chemicals has probably hidden the importance of other communication channels in social recognition. In particular, the possible influence of visual cues remained rather under estimated for many decades but the last 10–15 years saw an increasing attention toward the visual channel with various theoretical and experimental researches, especially in *Polistes* and stenogastrine wasps. Despite only few social wasp species have been investigated for the use of visual cues in some types of social recognition, almost all showed this ability, suggesting that this ability could be widely widespread in social wasps.

The independent evolution of this ability in Stenogastrinae and *Polistes* and the use of these cues for different purposes in different species (e.g. familiar recognition or badge of status) suggest moreover that social and ecological pressure might easily overcome physiological/phylogenetic constraints, allowing social wasps to rapidly evolve specific social recognition systems based on visual cues.

From an evolutionary point of view, the likelihood of evolving this recognition ability will be favoured by low constraints (e.g. physiological, such as low signal production costs and low complexity of the required perceptual ability) and by a high selective pressure (i.e. high benefits associated with the presence and use of visual cues). Despite the very limited knowledge about the signal production and perception mechanisms, some evidences suggest that both production and perception of visual signals (body markers) would be not so costly in social wasps. While the influences of nutritional and climatic factors seem to be important for the development of the signal, its production seems quite cheap for the individual and different patterns seem to have low differential production costs (Tibbetts and Dale 2004).

Regarding visual signal perception, despite a limited knowledge of the process, it seems evident that particular well developed recognition abilities are not required. Mini brain of insects are well equipped to visual cognitive task (Avargues-Weber et al. 2011) and analyses of neuronal networks showed that even complex tasks, such as face recognition, can be achieved with only a few hundreds neurons (Aitkenhead and McDonald 2003). Moreover, neuroanatomical analyses showed that, despite the possible presence of some neural specialization in species showing visual recognition abilities, paper wasps might be preadapted for visual pattern discrimination (Gronenberg et al. 2008). It is indeed likely that neural circuitry similar to that used by insects for prey recognition and navigation was fairly sufficient also for social recognition and was co-opted (and maybe only slighty re-wired) by those social insects species experiencing pertinent selection pressures (Gronenberg et al. 2008; Chittka and Dyer 2012). The ability of using visual cues to recognize social partners should not surprise. Indeed, social insects seem to have a quite good visual acuity, and "minibrains" of Hymenoptera have been shown to be keen on many visual tasks, from simple to complex ones (Avargues-Weber et al. 2011). Recent evidence moreover suggests that visual perception may have specifically coevolved with visual signalling in *Polistes* genus (Sheehan et al. 2014)

Despite much attention has been paid to propose and discuss possible selective pressures favouring the evolution of different types of visual recognition in social wasps (discussed in previous sections), reliable estimation of fitness benefits associated with visual recognition in different species and contexts has not been performed for most of the recognition types. For example, facial patterns in *P. dominula* have been shown to be not linked to any adaptive value in the wild (Green and Field Green et al. 2013). So far, the link between facial pattern and fitness benefits has been proved only in *P. fuscatus*, where wasps with variable faces that allow recognition receive less aggression than wasps which have with common indistinguishable faces (Sheehan and Tibbetts 2009). Future studies should focus on proximate and ultimate factors to reveal mechanisms, benefits and costs of visual recognition systems that may have triggered their evolution (Chapuisat 2004). While our knowledge on the matter is now increased, we are quite far from having a complete and clear picture and, as shown in the corresponding sections on this review, both visual signalling of badge of status and visual IR still deserve attention and further experimental approaches to understand the underlying processes and their evolutionary importance (Green et al. 2013; Gherardi et al. 2012; Chapuisat 2004; Wiley 2013). A major target of future researches should be to understand how visual cues interact with cues from other sensory channels, especially chemical ones (e.g. Boyle and Tricas 2014). It is possible that *Polistes* wasps can use chemicals or visual cues in different situations/contexts. Cuticular hydrocarbons blend and visual facial markers are contemporaneously bear by individual wasps so it is not easy to evaluate when and in which context chemicals or visual signals are used to convey the necessary information. At the moment, very few studies have been carried out (but see Ortolani et al. 2010; Cappa 2012; Baracchi et al. 2015) to evaluate the relative importance of a communicative channel over the other in a given context. Experiments to decouple visual and chemical signals should be necessary for completely understanding the communication system in primitively wasps. On the other hand, as chemical communication play an overwhelming importance in social insect life, a key aspect would be to understand whether chemical and visual stimuli interact in allowing specific type of recognition (e.g. familiar, individual, quality), and eventually how they contribute to build multimodal signals.

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References

Aitkenhead M, McDonald AJS (2003) A neural network face recognition system. Artif Intell 16:167–176

Andersson M, Simmons LW (2006) Sexual selection and mate choice. Trends Ecol Evol 21:296–302

Avarguès-Weber A, Deisig N, Giurfa M (2011) Visual cognition in social insects. Annu Rev Entomol 56:423–443

Baracchi D, Petrocelli I, Cusseau G, Pizzocaro L, Teseo S, Turillazzi S (2013) Facial markings in the hover wasps: quality signals and familiar recognition cues in two species of Stenogastrinae. Anim Behav 85:203–212

Baracchi D, Petrocelli I, Chittka L, Ricciardi G, Turillazzi S (2015) Speed and accuracy in nest-mate recognition: an hover wasp prioritizes face recognition over colony odour cues to minimize intrusion by outsiders. Proc R Soc B 282 (1802): 20142750 doi:10.1098/rspb.2014.2750

Batra SWT (1980) Sexual behaviour and pheromones of the European hornet, *Vespa crabro* germana (Hymenoptera: Vespidae). J Kansas Entomol Soc 53:461–469

Beani L (1996) Leklike courtship in paper wasps: “A prolonged, delicate, and troublesome affair”. In: Turillazzi S, West-Eberhard MJ (eds) The natural history and evolution of paper-wasps. Oxford University Press, Oxford, pp 113–125

Beani L, Turillazzi S (1988) Alternative mating tactics in males of *Polistes dominulus* (Hymenoptera: Vespidae). Behav Ecol Sociobiol 22:257–264

Beani L, Turillazzi S (1994) Aerial patrolling and stripes display in males of *Parischnogaster mellyi* (Hymenoptera Stenogastrinae). Ethol Ecol Evol Spec Issue 3:43–46

Beani L, Turillazzi S (1999) Stripes display in hover-wasps (Vespidae: Stenogastrinae): a socially costly status badge. Anim Behav 57:1233–1239

Beani L, Cervo R, Lorenzi MC, Turillazzi S (1992) Landmark-based mating systems in four *Polistes* species (Hymenoptera, Vespidae). J Kansas Entomol Soc 65:211–217

Beecher MD (1989) Signalling systems for individual recognition: an information theory approach. Anim Behav 38:248–261

Berglund A, Bisazza A, Pilastro A (1996) Armaments and ornaments: an evolutionary explanation of traits of dual utility. Biol J Linn Soc 58:385–399

Bourke AFG (1999) Colony size, social complexity and reproductive conflict in social insects. J Evol Biol 12(2):245–257

Boyle KS, Tricas TC (2014) Discrimination of mates and intruders: visual and olfactory cues for a monogamous territorial coral reef butterflyfish. Anim Behav 92:33–43

Buck M, Cobb TP, Stahlhut JK, Hanner RH (2012) Unravelling cryptic species diversity in eastern Nearctic paper wasps, *Polistes (Fuscopolistes)*, using male genitalia, morphometrics and DNA barcoding, with descriptions of two new species (Hymenoptera: Vespidae). Zootaxa 3502:1–48

Cappa F (2012) The male phenotype in *Polistes dominula*: sexual selection and host-parasite interactions. PhD thesis, University of Florence

Cervo R (1994) Morphological adaptations to the parasitic life in *Polistes sulcifer* and *P. atrimandibularis* (Hymenoptera Vespidae). Ethol Ecol Evol 6:61–66

Cervo R (2006) *Polistes* wasps and their social parasites: an overview. Ann Zool Fenn 43:531–549

Cervo R, Dani FR (1996) Social parasitism and its evolution in *Polistes*. In: Turillazzi S, West-Eberhard MJ (eds) The natural history and evolution of paper-wasps. Oxford University Press, Oxford, pp 98–112

Cervo R, Zacchi F, Turillazzi S (2000) *Polistes dominulus* (Hymenoptera, Vespidae) invading North America: some hypothesis for its rapid spread. Insectes Soc 47:155–157

Cervo R, Stemmer C, Castle W, Queller D, Strassmann JE (2004) Social parasitism of *Polistes dominulus* by *Polistes nimphus* (Hymenoptera, Vespidae). Insectes Soc 51(2):101–108

Cervo R, Dapporto L, Beani L, Strassmann JE, Turillazzi S (2008) On status badges and quality signals in *Polistes dominulus*: body size, facial colour patterns and hierarchical rank. Proc R Soc London B 275:1189–1196

Chapuisat M (2004) Evolution: social selection for eccentricity. Curr Biol 14:R1003–R1004

Chittka L, Dyer A (2012) Your face looks familiar. Nature 481:154–155

Choudary M, Strassmann JE, Queller DC, Turillazzi S, Cervo R (1994) Social parasites in Polistine wasps are monophyletic: implications for sympatric speciations. Proc R Soc London B 257:31–35

Cini A, Bruschini C, Poggi L, Cervo R (2011) Fight or fool? Physical strength, instead of sensory deception, matters in host nest invasion by a wasp social parasite. Anim Behav 81(6):1139–1145

Cini A, Nieri R, Dapporto L, Monnin T, Cervo R (2014) Almost royal: incomplete suppression of host workers ovarian development b a social parasite wasp. Behav Ecol Sociobiol 68(3): 467–475. doi:10.1007/s00265-013-1661-z

Cini A, Ortolani I, Zechini L, Cervo R (2015) Facial markings in the social cuckoo wasp *Polistes sulcifer*: no support for the visual deception and the assessment hypotheses. Behav Process 111:19–24. doi:10.1016/j.beproc.2014.11.010

Dale J, Lank DB, Reeve HK (2001) Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. Am Nat 158:75–86

Dani FR, Cervo R (1992) Reproductive strategies following nest loss in *Polistes gallicus* (Hymenoptera, Vespidae). Ethol Ecol Evol Spec Issue 2:49–53

Dapporto L, Pansolli C, Turillazzi S (2004) Hibernation clustering and its consequences for associative nest foundation in *Polistes dominulus* (Hymenoptera Vespidae). Behav Ecol Sociobiol 56(4):315–321

de Souza AR, Júnior CAM, do Nascimento FS, Lino-Neto J (2014) Sexy faces in a male paper wasp. PLoS One 9(5):e98172

Gamboa GJ, Greig EI, Thom MC (2002) The comparative biology of two sympatric paper wasps, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). Insectes Soc 49(1):45–49

Gherardi F, Aquiloni L, Tricarico E (2012) Revisiting social recognition systems in invertebrates. Anim Cogn 15(5):745–762

Green JP, Field J (2011a) Interpopulation variation in status signalling in the paper wasp *Polistes dominulus*. Anim Behav 81:205–209

Green JP, Field J (2011b) Assessment between species: information gathering in usurpation contests between a paper wasp and its social parasite. Anim Behav 81(6):1263–1269

Green JP, Rose C, Field J (2012) The role of climatic factors in the expression of an intrasexual signal in the paper wasp *Polistes dominulus*. Ethology 118(8):766–774

Green JP, Leadbeater E, Carruthers JM, Rosser NS, Lucas ER, Field J (2013) Clypeal patterning in the paper wasp *Polistes dominulus*: no evidence of adaptive value in the wild. Behav Ecol 24(3):623–633

Gronenberg W, Ash LE, Tibbetts EA (2008) Correlation between facial pattern recognition and brain composition in paper wasps. Brain Behav Evol 71:1–14

Guerrieri FJ, d'Ettorre P, Devaud JM, Giurfa M (2011) Long-term olfactory memories are stabilised via protein synthesis in *Camponotus fellah* ants. J Exp Biol 214:3300–3304

Halpin ZT (1980) Individual odors and individual recognition: review and commentary. Biol Behav 5:233–248

Howard RW, Blomquist GJ (2005) Ecological, behavioral, and biochemical aspects of insect hydrocarbons. Annu Rev Entomol 50:371–393

Hunt JH, Richard FJ (2013) Intracolony vibroacoustic communication in social insects. Insectes Soc 60(4):403–417

Izzo AS, Tibbetts EA (2012) Spotting the top male: sexually selected signals in male *Polistes dominulus* wasps. Anim Behav 83:839–845

Kirchner WH (1997) Acoustical communication in social insects. In: *Orientation and communication in Arthropods*. Birkhäuser Basel, Switzerland, pp 273–300

Lai WS, Ramiro LLR, Helena AY, Johnston RE (2005) Recognition of familiar individuals in golden hamsters: a new method and functional neuroanatomy. J Neurosci 25(49):11239–11247

Liebert AE, Gamboa GJ, Stamp NE, Curtis TR, Monnet KM, Turillazzi S, Starks PT (2006) Genetics, behavior and ecology of a paper wasp invasion: *Polistes dominulus* in North America. Ann Zool Fenn 43:595–624

Lorenzi MC (2006) The result of an arms race: the chemical strategies of *Polistes* social parasites. Ann Zool Fenn 43:550–563

Lorenzi MC, Caprio P (2000) Nest recognition in neighboring colonies: a comparison of two European species of *Polistes* wasps (*P. dominulus* and *P. nimphus*, Hymenoptera: Vespidae). J Ethol 18(2):65–68

Nieh JC (2004) Recruitment communication in stingless bees (Hymenoptera, Apidae, Meliponini). Apidologie 35:159–182

Ortolani I, Cervo R (2009) Coevolution of daily activity timing in a host–parasite system. Biol J Linn Soc 96(2):399–405

Ortolani I, Cervo R (2010) Intra-specific body size variation in *Polistes* paper wasps as a response to social parasite pressure. Ecol Entomol 35(3):352–359

Ortolani I, Turillazzi S, Cervo R (2008) Spring usurpation restlessness: a wasp social parasite adapts its seasonal activity to the host cycle. Ethology 114(8):782–788

Ortolani I, Zecchini L, Turillazzi S, Cervo R (2010) Recognition of a paper wasp social parasite by its host: evidence for a visual signal reducing host aggressiveness. Anim Behav 80:683–688

Pagden HT (1962) More about Stenogaster. Malayan Nat J 16:95–102

Pardi L (1948) Dominance order in *Polistes* wasps. Physiol Zool 21:1–13

Petrocelli I, Turillazzi S (2013) Comparative morphology of Van der Vecht’s organ in *Polistes* social parasites: host ecology and adaptation of the parasite. Biol J Linn Soc 109(2):313–319

Petrocelli I, Ricciardi G, Rodrigues de Souza A, Ermanni A, Ninu A, Turillazzi S (2014) Visual signals of individual quality in a European solitary founding paper wasp. Ethology 121(3): 300–307. doi:10.1111/eth.12339

Queller DC, Zacchi F, Cervo R, Turillazzi S, Henshaw MT, Santorelli LA, Strassmann JE (2000) Unrelated helpers in a social insect. Nature 405:784–787

Reeve HK (1991) *Polistes*. In: Ross KG, Matthews RW (eds) The social biology of wasps. Ithaca, Comstock, pp 99–148

Rohwer S (1975) The social significance of avian winter plumage variability. Evolution 29:593–610

Rohwer S (1977) Status signalling in Harris’ sparrows. Behaviour 61:107–129

Roper T (1986) Badges of status in avian societies. New Sci 109:38–40

Senar JC, Camerino M (1998) Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*). Proc R Soc London B 265:1515–1520

Sheehan MJ, Tibbetts EA (2008) Robust long-term social memories in a paper wasp. Curr Biol 18(18):R851–R852

Sheehan MJ, Tibbetts EA (2009) Evolution of identity signals: frequency dependent benefits of distinctive phenotypes used for individual recognition. Evolution 63(12):3106–3113

Sheehan MJ, Tibbetts EA (2011) Specialized face learning is associated with individual recognition in paper wasps. Science 334(6060):1272–1275

Sheehan MJ, Jinn J, Tibbetts EA (2014) Coevolution of visual signals and eye morphology in *Polistes* paper wasps. Biol Lett 10(4):20140254

Smith JM, Harper DGC (1988) The evolution of aggression: can selection generate variability? Philos Trans R Soc B 319:557–570

Smith JM, Harper D (2003) Animal signals. Oxford University Press, Oxford

Spiewok S, Schmolz E, Ruther J (2006) Mating system of the European hornet *Vespa crabro*: male seeking strategies and evidence for the involvement of a sex pheromone. J Chem Ecol 32:2777–2788

Starks PT, Turillazzi S, West-Eberhard MJ (2006) *Polistes* paper wasps: emergence of a model genus. Ann Zool Fenn 43(5–6):385–386

Steiger S, Müller JK (2008) 'True'and 'untrue'individual recognition: suggestion of a less restrictive definition. Trends Ecol Evol 23(7):355

Strassmann JE (2004) Animal behaviour: rank crime and punishment. Nature 432(7014):160–162

Tannure-Nascimento IC, Nascimento FS, Zucchi R (2008) The look of royalty: visual and odour signals of reproductive status in a paper wasp. Proc R Soc London B 275:2555–2561

Thom MD, Hurst JL (2000) Individual recognition by scent. Ann Zool Fenn 41:765–787

Tibbetts EA (2002) Visual signals of individual identity in the wasp *Polistes fuscatus*. Proc R Soc London B 269(1499):1423–1428

Tibbetts EA (2006a) Badges of status in workers and gyne *Polistes dominulus* wasps. Ann Zool Fenn 43:575–582

Tibbetts EA (2006b) The condition-dependence and hereditability of signaling and non-signalling color traits in the paper wasps. Am Nat 175:495–503

Tibbetts EA (2008) Resource value and the context dependence of receiver behaviour. Proc R Soc London B 275:2201–2206

Tibbetts EA, Curtis TR (2007) Rearing conditions influence quality signals but not individual identity signals in *Polistes* wasps. Behav Ecol 18(3):602–607

Tibbetts EA, Dale J (2004) A socially enforced signal of quality in a paper wasp. Nature 432(7014):218–222

Tibbetts EA, Dale J (2007) Individual recognition: it is good to be different. Trends Ecol Evol 22(10):529–537

Tibbetts EA, Injaian A (2013) Preferential phenotypic association linked with cooperation in paper wasps. J Evol Biol 26:2350–2357

Tibbetts EA, Lindsay R (2008) Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. Biol Lett 4(3):237–239

Tibbetts EA, Sheehan MJ (2011) Facial patterns are a conventional signal of agonistic ability in *Polistes exclamans* paper wasps. Ethology 117(12):1138–1146

Tibbetts EA, Shorter JR (2009) How do fighting ability and nest value influence usurpation contests in *Polistes* wasps? Behav Ecol Sociobiol 63:1377–1385

Tibbetts EA, Sheehan MJ, Dale J (2008) A testable definition of individual recognition. Trends Ecol Evol 23:356

Tibbetts EA, Mettler A, Levy S (2010) Mutual assessment via visual status signals in *Polistes dominulus* wasps. Biol Lett 6(1):10–13

Tibbetts EA, Izzo A, Huang ZY (2011a) Behavioral and physiological factors associated with juvenile hormone in *Polistes* wasp foundresses. Behav Ecol Sociobiol 65(5):1123–1131

Tibbetts EA, Skadina O, Zhao V, Thot AL, Skaldin M, Beani L, Dale J (2011b) Geographic variation in the status signals of *Polistes dominulus* paper wasps. PLoS One 6:e28173

Toth AL, Bilof KBJ, Henshaw MT, Hunt JH, Robinson GE (2009) Lipid stores, ovary development, and brain gene expression in *Polistes metricus* females. Insectes Soc 56:77–84

Turillazzi S (2012) The biology of hover wasps. Springer, Berlin

Turillazzi S, Cervo R (1982) Territorial behaviour in males of *Polistes nimpha* (Christ) (Hymenoptera, Vespidae). Zeitschrift für Tierpsychologie 58:174–180

Van Zweden JS, d'Ettorre P (2010) Nestmate recognition in social insects and the role of hydrocarbons. In: Blomquist GJ, Bagnères AG (eds) Insect hydrocarbons: biology, biochemistry and chemical ecology. Cambridge University Press, Cambridge, pp 222–243

Whiting MJ, Nagy KA, Bateman PW (2003) Evolution and maintenance of social status-signaling badges. Experimental manipulations in lizards. In: Fox SF, McCoy JK, Baird TA (eds) Lizard social behavior. JHU Press, Baltimore, pp 47–82

Wiley RH (2013) Specificity and multiplicity in the recognition of individuals: implication for the evolution os social behaviour. Biol Rev 88:179–195

Wilson EO (1971) The insect societies. Harvard University Press, Cambridge, p 548

Zanette L, Field J (2009) Cues, concessions, and inheritance: dominance hierarchies in the paper wasp *Polistes dominulus*. Behav Ecol 20(4):773–780