Animal Behaviour 85 (2013) 203–212

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Facial markings in the hover wasps: quality signals and familiar recognition cues in two species of Stenogastrinae

D. Baracchi [a,*], I. Petrocelli [a], G. Cusseau [a], L. Pizzocaro [a], S. Teseo [b], S. Turillazzi [a]

[a] *Università degli Studi di Firenze, Dipartimento di Biologia Evoluzionistica 'Leo Pardi', Firenze, Italy*
[b] *Université Paris 13, Laboratoire d'Ethologie Expérimentale et Comparée, EA 4443, Paris, France*

ARTICLE INFO

Article history:
Received 28 June 2012
Initial acceptance 23 July 2012
Final acceptance 9 October 2012
Available online 21 November 2012
MS. number: 12-00501R

Keywords:
animal communication
badge of status
conventional signal
dominance hierarchy
hover wasp
Liostenogaster flavolineata
Liostenogaster vechti
quality signal
recognition system
social behaviour

Both recognition and conventional signals are widespread in the animal kingdom. Chemical communication plays a major role in invertebrates, and especially in social insects. In the last decade, observational and experimental evidence has shown the existence of visual quality signals and individual recognition cues in *Polistes* paper wasps, meaning that visual communication might also be common in insect societies. Here we show that two species of facultatively eusocial hover wasps (Vespidae, Stenogastrinae) use the visual channel for social communication. By combining morphoanatomical measurements and behavioural assays, we found that the size of the dark facial markings was related to reproductive status and dominance in colonies of *Liostenogaster vechti*, thus representing a badge of status. By contrast, no correlation between facial coloration and reproductive status was found in *Liostenogaster flavolineata*, which instead used facial markings as familiar visual recognition cues. Our results reveal that visual communication in social insects might be more widespread than previously thought and has evolved independently in distinct wasp taxa facing similar selection pressures.

Members of animal societies need to cooperate and coordinate group behaviours. Efficient communication systems as well as recognition abilities are required for almost all social behaviours. Nestmate recognition, that is, the ability of an individual to recognize its colony mates, is critical to prevent outsiders from exploiting colony resources (Hölldobler & Wilson 1990). Discriminating between different colony mates allows individuals to adjust their behaviours, which is fundamental for assessing and maintaining dominance hierarchies and regulating parent–offspring interactions. Most social species can discriminate between conspecifics for several characteristics, which include reproductive status, hierarchical rank, familiarity, group membership, kinship and individual identity (Thom & Hurst 2004).

In class-level recognition, conspecifics are assigned to the appropriate class by using a relatively simple distinction between limited alternatives, such as 'male' versus 'female', 'familiar' versus 'unfamiliar', 'group member' versus 'nongroup member'. Signals that are relatively uniform for individuals within a class, but relatively distinct from the overall population, are usually involved in these processes (Tibbetts & Dale 2007). For individual recognition the evaluator learns the individually distinctive characteristics of the cue-bearer, which are predicted to be (1) variable enough to allow accurate discrimination between individuals and (2) not dependent on health (Dale et al. 2001). In contrast to identity signals, quality signals require high, differential costs to maintain an honest association with true quality (Zahavi 1975; Getty 2006). Unlike most sexual signals, which have production-related costs, several fighting ability signals have only social costs associated with their maintenance (Rohwer 1975; Maynard Smith & Harper 1988; Senar 1999, 2006; Gil & Gahr 2002; Whiting et al. 2003; Tibbetts & Dale 2004). These 'area' signals are often termed 'conventional' or 'badges of status' (Guilford & Dawkins 1995). Recent studies suggest that rank markings must be costly to their bearers because only high-quality individuals can support the social costs of increased aggression from other individuals (reviewed in Jawor & Breitwisch 2003).

Both recognition and conventional signals are common in the animal kingdom and they occur in many different modalities, including olfactory, visual and acoustic (reviewed in Dale et al. 2001). Several studies have shown that visual signals evolved as badges of status or recognition cues in many vertebrates (reviewed in Senar

* Correspondence: D. Baracchi, Università degli Studi di Firenze, Dipartimento di Biologia Evoluzionistica 'Leo Pardi', Via Romana 17, 50125 Firenze, Italy.
E-mail address: david.baracchi@gmail.com (D. Baracchi).

0003-3472/$38.00
http://dx.doi.org/10.1016/j.anbehav.2012.10.027

1999; Whiting et al. 2003; Setchell & Wickings 2005). Furthermore, even if invertebrates, and in particular social insects, primarily use chemical cues for communication (reviewed in Vander Meer et al. 1998; Howard & Blomquist 2005) both observational and experimental evidence has shown that they are also able to use the visual channel (Shreeve 1987; Karavanich & Atema 1998; Beani & Turillazzi 1999; Tibbetts 2002; Tibbetts & Dale 2004). The paper wasps *Polistes fuscatus* and *Polistes dominulus* have variable cuticular markings that are used for social communication. Despite their similarities, the signals of these two species apparently convey completely different information. Experiments in which facial and abdominal markings of *P. fuscatus* females were manipulated suggest that workers and gynes use these features to recognize individual nestmates (Tibbetts 2002). In contrast, according to Tibbetts & Dale (2004) the complexity (brokenness) of facial markings of *P. dominulus* females in a North American population conveys information on their agonistic qualities. Tibbetts & Dale (2004) suggested that the cost of this badge is not due to pigment production, since it represents only 1% of the total body pigment, but to the social costs that it entails. In contrast, this badge of status is absent in the nesting foundresses of an Italian population (Cervo et al. 2008). Furthermore, although Zanette & Field (2009) did report a correlation between facial markings and dominance in a Spanish population, this was no longer significant when other factors (e.g. intragroup relatedness) were also considered. In this case the hypothesis is that badges of status are one of various factors that can influence dominance hierarchies and reproductive skew (Zanette & Field 2009). Owing to the differences between these populations, many controversies in the literature revolve around the role of visual signals in wasps (see Strassmann 2004; Cervo et al. 2008). Information on visual communication is also available for other genera not closely related to *Polistes* wasps. For example, a status signal was described and studied by Beani & Turillazzi (1999) in males of *Parischnogaster mellyi* (Vespidae, Stenogastrinae), which use it during flying duels for winning a perch in aerial leks. Beani & Turillazzi (1999) found that males were increasingly challenged by contenders when given an extra visual signal represented by an additional white stripe painted on the back of their gasters.

The Stenogastrinae, or hover wasps, represent a taxon of 58 described species in seven genera inhabiting the forests of South-East Asia (Turillazzi 1991; Carpenter & Kojima 1996). They have small colonies (maximum 10 females) in which recognition, up to the individual level, might be useful for social organization. In the genera *Liostenogaster*, *Eustenogaster* and *Parischnogaster* various species present highly variable facial markings, potentially allowing the use of visual cues. Both *Liostenogaster vechti* and *Liostenogaster flavolineata* (two of the most common species) have a peculiar nesting biology with many colonies forming large aggregations, sometimes with hundreds of nests built within 5 cm of one other. As a consequence, colonies in clusters experience continuous landing attempts by neighbouring, alien individuals, which are sometimes received peacefully (Samuel 1987; Turillazzi et al. 1997; Coster-Longman 1998). Zanetti et al. (2001) observed how the hesitant approaching flights of landing individuals can elicit an alarm reaction from the residents of colonies of *Parischnogaster striatula*, just before recognition based on chemical cues could trigger aggressive reactions. These reports suggest a possible involvement of facial markings in the recognition process in both *L. vechti* and *L. flavolineata*.

The aim of our study was to determine whether visual communication could be important in the social organization of *L. flavolineata* and *L. vechti*. We first measured the head width (a reliable indicator of body size) and size of facial markings of female wasps collected in the field, checking for a relation of these features with ovarian development and social rank. Based on the results obtained in the first part of the study we tested whether (1) *L. vechti* females use their facial markings as quality signals to assess the value of conspecifics, and (2) *L. flavolineata* females are able to use facial markings of nestmates as visual recognition cues.

METHODS

Studied Species

Liostenogaster vechti forms colonies with up to seven females on a bracket-like or ringed nest (Turillazzi 1990). Colonies of this species are usually found in large clusters (up to more than 600 nests) on the walls of buildings, caves or overhanging rocks. For this species, Cervo et al. (1996) reported a nestmate recognition ability based on chemical cues, and Turillazzi (1990) found that, only one or two potentially egg-laying females per nest are usually present.

Liostenogaster flavolineata is one of the best-known species in the group. It builds mud comb nests with up to more than 100 cells, sometimes in huge aggregates (Hansell 1982; Samuel 1987). Similarly to *L. vechti*, chemical nestmate recognition in this species has been reported and studied by Cervo et al. (1996, 2002). Social groups are relatively small (up to 10 females) and newly emerged females may disperse or become helpers on their natal nests. Bridge (2005) and Bridge & Field (2007) reported the existence of a queue for dominance based on gerontocracy (dominance order is age-based: in a nest a subordinate inherits dominance only when all her older relatives have disappeared). Field & Foster (1999) and Sumner et al. (2002) found on average only one egg-laying female per nest and only 8% of nondominant females with developed ovaries.

Sample Collection

Twenty-five colonies of *L. vechti* with a total of 76 females (mean: 3.0 females per colony, range 2–5) and 30 colonies of *L. flavolineata* with a total of 97 females (mean: 3.2 females per colony, range 2–5) were collected from two different sites: Bukit Fraser (1000 m above sea level) and Genting Tea Estate (610 m above sea level) in the Pahang State of Peninsular Malaysia. We killed all the wasps at −20 °C before measuring head width, ovarian development and facial markings (see below).

Morphological Measurements and Facial Pattern Categorization

We took a picture of the 'face' of each collected wasp with a Fujifilm digital camera (Fig. 1). A body size estimate was then obtained by measuring the maximum width of the head (Eickwort 1969). We dissected the ovaries of all females under a binocular microscope to determine their reproductive status. For each individual, the ovarian status was quantified by using an ovarian index (OI) based on the development of the ovaries. This was performed by taking a picture using a Fujifilm camera and by measuring the length of the six largest oocytes present in the ovarioles. Since usually only the dominant female lays eggs, she possesses the most developed ovaries in her colony. The OI is thus a meaningful rank estimator. We also checked the spermatheca of each female for the presence of sperm. To categorize the facial patterns of females in both species we measured the size of the brown pigmented area on the faces (facial marking size, FMS; see also Zanette & Field 2009). All measurements were made on digital photographs by using the free software ImageJ (http://rsbweb.nih.gov/ij/). We took into account only the area corresponding to the clypeus plus eyebrows (dorsal to the antennal sockets region) since it includes most of the variability in the wasps' facial markings. Inner and outer eye stripes, antennae and mandibles were ignored as they were yellow in all the specimens of both species (see Appendix Fig. A1). To avoid the bias from individuals with a high FMS but still too young to develop ovaries and reproduce, further statistical analyses were performed only for individuals