# Facial patterns in a tropical social wasp correlate with colony membership

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Abstract Social insects excel in discriminating nestmates from intruders, typically relying on colony odours. Remarkably, some wasp species achieve such discrimination using visual information. However, while it is universally accepted that odours mediate a group level recognition, the ability to recognise colony members visually has been considered possible only via individual recognition by which wasps discriminate 'friends' and 'foes'. Using geometric morphometric analysis, which is a technique based on a rigorous statistical theory of shape allowing quantitative multivariate analyses on structure shapes, we first quantified facial marking variation of Liostenogaster flavolineata wasps. We then compared this facial variation with that of chemical profiles (generated by cuticular hydrocarbons) within and between colonies. Principal component analysis and discriminant analysis applied to sets of variables containing pure shape information showed that despite appreciable intra-colony variation, the faces of females belonging to the same colony resemble one another more than those of outsiders. This colony-specific

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variation in facial patterns was on a par with that observed for odours. While the occurrence of face discrimination at the colony level remains to be tested by behavioural experiments, overall our results suggest that, in this species, wasp faces display adequate information that might be potentially perceived and used by wasps for colony level recognition.

**Keywords** Face recognition · Insect cognition · Individual recognition · Nestmate recognition · Visual signals

#### Introduction

A number of vertebrate species such as members of the mammals (Halpin 1980), birds (Bonadonna and Nevitt 2004) and fish (Höjesjö et al. 1998), and invertebrates such as hermit crabs (Gherardi and Tiedemann 2004), social bees, ants and wasps (Barrows 1975; d'Ettorre and Heinze 2005; Tibbetts 2002) are known to recognise individual conspecifics. This ability is advantageous in diverse situations such as parental care in species with synchronous nesting [pinnipeds (Insley 2000; Charrier et al. 2003), bats (Balcombe 1990)], territoriality [penguins (Aubin and Jouventin 1998), songbirds (Godard 1991)], dominance interactions and aggressive competitions [insects (Tibbetts 2002; d'Ettorre and Heinze 2005), aquatic invertebrates (Karavanich and Atema 1998), fish (Höjesjö et al. 1998), monkeys (Silk 1999)]. In social animals, however, recognising members of a society or colony is often as important as individual recognition. In social insects, such colony level recognition is often mediated by odour cues (van Zweden and d'Ettorre 2010), though visual colony cues are likely to be used in some stingless bees that build unique colony nest entrance structures (Chittka et al. 1997).

In at least two subfamilies of wasps, visual recognition of individuals also plays a role in individual, rank and nestmate recognition (Beani and Turillazzi 1999; Tibbetts 2002;



Tibbetts and Dale 2004; Baracchi et al. 2013). Several paper and hover wasp species have variable facial and abdominal cuticular markings that are used for social communication (Cervo et al. 2015). For instance, *Polistes gallicus, Polistes exclamans, Polistes dominula* and *Liostenogaster vechti* females use black clypeal spots as conventional signals to convey information on their agonistic qualities such as dominance status and aggressiveness (Tibbetts and Dale 2004; Tibbetts and Sheehan 2011; Baracchi et al. 2013; Petrocelli et al. 2015). By contrast, experiments in which facial markings of *Polistes fuscatus* and *Liostenogaster flavolineata* females were experimentally manipulated indicate that workers can visually recognise individual nestmates (Tibbetts 2002; Baracchi et al. 2013).

So far, nestmate recognition via visual information has been considered possible only via individual recognition where individuals must remember the facial features of all colony members (Tibbetts 2002; Tibbetts and Dale 2007; Baracchi et al. 2013). However, at least in principle, all members of a colony might be identified as nestmates according to shared common features of their facial pattern.

In the wasp L. flavolineata, a species whose colonies rarely have more than six individuals, both vision and olfaction mediate nestmate recognition, and unfamiliar odours or faces induces residents to assault colony intruders (Baracchi et al. 2013, 2015). When the facial marking of conspecifics was experimentally altered by adding yellow or brown paint to the clypeus in order to slightly change its appearance, they were treated more aggressively than those with unaltered faces by resident nestmates (Baracchi et al. 2013). Vision seems to be prioritized by resident females over odours early in an encounter and olfactory cues are used later to enhance accuracy in the recognition process (Baracchi et al. 2015). This species builds small nests typically in large aggregations (Coster-Longman et al. 2002). As a consequence, landing attempts by neighbouring alien wasps, some of which are occasionally received peacefully, are quite frequent (Coster-Longman et al. 2002). Dominance order is age based and the older female monopolises reproduction until her death, while young females may disperse or become helpers on their natal nest queuing for inheriting dominance (Bridge and Field 2007). A previous study (Cervo et al. 2002) demonstrated that nestmates have more similar cuticular hydrocarbon profiles (CHCs) than non-nestmates, suggesting that CHCs can be effective cues to identify nest membership. By contrast, to date it is unknown whether wasps from the same colony have more similar facial patterns than do wasps from different colonies. As a consequence, it is unclear whether visual nestmate recognition is based on a common face pattern shared by nestmates by which all members of a colony can be identified or whether there is an individual recognition via facial markings which is used to recognise colony members. In the present work, we first determined whether facial patterns contain sufficient information about colony membership by quantifying within- and between-colony variation of faces. Then, we compared statistically this level of information with the one contained in the cuticular hydrocarbon profiles to determine face and odour potential reliability in discriminating between nestmate and alien wasps.

## **Materials and Methods**

Twelve colonies of L. flavolineata with a total of 44 females (mean: 3.5 females per colony, range 3-6) were collected in Malaysia (03° 42.774 N-101° 46.319 E). Morphometric analysis of the facial marking was used to describe withinand between-colony facial variation (Fig. 1a). The general procedure was similar to that used to classify stenogastrine species using wing morphology (Baracchi et al. 2011). We took pictures of the faces of each wasp with a Fujifilm AX550 digital camera under a stereo microscope. Fifty-six points on the face were chosen as landmarks (5) or semilandmarks (51) for geometric morphometrics, so that for each wasp we obtained a landmark configuration as the one showed in Fig. 1a. Landmarks correspond to evolutionarily homologous anatomical parts that are the same in all the specimens (i.e. the tip of the clypeus, the upper joint of the left and the right mandibles and the left and the right ends of the front in its widest point, Fig. 1a). Semilandmarks are non-homologous points (i.e. points whose position along a curve is arbitrary but which provide information about the curvature of the silhouette of clypeal marking, Fig. 1a). By definition, a shape consists in all the geometric features of an object except for its size, position and orientation in the space (Dryden and Mardia 1998). Wasp faces have different sizes and differed slightly also in their orientation and location in the pictures. In order to compare the shape of the clypeal markings, we removed all these non-shape information using a standard statistical method commonly used in geometric morphometrics (i.e. the generalized procrustes analysis (GPA, (Gower 1975))), which allows to superimpose a population of shape instances annotated by landmark and semi-landmark points in a common coordinate system (Rohlf and Slice 1990). Precisely, by translating, rotating and scaling the pictures of the faces to find the best fit between landmark shapes and to minimize the differences between them, the generalized procrustes analysis optimally aligned and superimposed the facial markings and extracted sets of variables containing pure shape information called partial warps (PWs). A principal component analysis (PCA) was applied to the PWs in order to convert these set of possibly correlated variables into a lower number of uncorrelated variables called relative warps (RWs). Shape variation in the facial markings can be visualized by entering the RWs in the thin-plate-spline

Fig. 1 a Landmarks (in red) and semi-landmarks (in *blue*) positioned on the face of 44 L. flavolineata females. b-e Variation in shape of the female facial marking. The red lines connect semi-landmarks (facial marking) while the black lines connect landmarks. b, c represent facial markings of hypothetical wasps located at the *left* and the right ends of the RW1 axis (Fig. ESM2). d, e represent facial markings of hypothetical wasps located at the top and the bottom edge of the RW2 axis







deformation grids (i.e. a mathematically rigorous implementation of D'Arcy Thompson's Cartesian transformation grids (Bookstein 1989), Fig. 1b-e). To give a visual representation of the average facial marking of three colonies, we first computed the mean RW1 and RW2 as the geometric centroid of the RW1 and RW2 belonging to all the wasps of each colony. We then entered these two RWs in the thinplate-spline deformation grids. All the analyses were carried out using the TPS series of software (Rohlf 2015). Published data on chemical profiles obtained for 12 additional colonies from the same location (n = 41 wasps, 3.5 females on aver-)age per colony, range 2-5) of L. flavolineata (Cervo et al. 2002) were used for a direct statistical comparison with our morphological data. Principal component analysis (PCA) and discriminant analysis (DA) applied to the variables containing chemical (PCs) and morphological information (RWs) were used to assess the extent to which facial pattern and chemical profile provide good cues for nestmate recognition. In order to obtain a conservative output for the DA, we performed a full cross-validation test (CV test) using the leave-one-out technique (Baracchi et al. 2010). All analyses were performed using Paws Statistics 19.00 (Chicago, IL, USA).

### Results

Twenty-seven chemical compounds were identified on the cuticle of the wasps (Cervo et al. 2002). The PCA applied to those compounds extracted five PCs (functions of variables

containing chemical information) that explained 78 % of the total variance in our sample when combined. PCA applied to the shape variables extracted 59 relative warps (RWs, functions of variables containing shape information). To be more conservative, since the PCA applied on chemical data provided only five PCs, we used the same number of RWs (explaining a cumulative variance of 75 %) for successive analyses.

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PC<sub>1</sub> and PC<sub>2</sub> explained 28.0 and 21.6 % of variance of the chemical profiles (Fig. ESM 1) while RW<sub>1</sub> and RW<sub>2</sub> explained 45.8 and 10.1 % of variance of the facial markings (Fig. ESM 2), respectively. These percentages suggest that, regardless of colony membership, the variation of both the chemical profiles and the facial markings in the overall population is similar although they represent two completely different types of cue. The variation in the facial marking in the studied population is illustrated by deformation grids (Fig. 1). The RW<sub>1</sub> indicated that almost half of the variation (45.8 %) in the facial markings is due to the different top-to-bottom length of the brownish marking along the vertical axis of the clypeus (Fig. 1b, c). In particular, at the one end of the variation along the RW<sub>1</sub>, there are wasps with the two external cusps far longer than the one in the middle (Fig. 1b), while at the other end there are wasps whose facial marking almost entirely lacks the two external cusps and has the middle one more prominent (Fig. 1c). A clear example of this latter facial pattern is represented by some females belonging to colony 1 reported in Fig. 3. The RW<sub>2</sub>, which is the second most important function explaining about the 10 % of the facial variation in our population, mainly reassumed the variation along the

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horizontal axis of the clypeus at the level of both the three cusps and the junction between the upper end of the clypeus and the lower end of the front, where the facial marking extends to and above the antennal sockets. Precisely, at one end of the variation along the RW<sub>2</sub>, there are wasps with a quite narrow facial marking at the level of the frontal-clypeal junction but a wide trident composed of three long cusps of equal length (Fig. 1e). At the other end of RW<sub>2</sub> variation, there are wasps with an evident square facial marking and a much reduced length of the three cusps (Fig. 1d). The individuals belonging to colony 3 shown in Fig. 3 are clear examples of this latter condition.

DA correctly assigned 58.5 % (26.8 % in the CV test) of the females to their colony using CHC profiles (function 1: Wilks'  $\lambda = 0.022$ , P < 0.001, explained variance 43.8 %; function 2: Wilks'  $\lambda = 0.084$ , P < 0.001, explained variance 25.8 %, Fig. 2) and 61.4 % (25 % in CV test) of females to their colony using facial markings (function 1: Wilks'  $\lambda = 0.034, P < 0.001$ , explained variance 52.1 %; function 2: Wilks'  $\lambda = 0.014$ , P = 0.004, explained variance 28.1 %, Fig. 2) indicating that within- and between-colony variation of the facial patterns and the chemical profiles are similar. Some examples of the variation in the facial marking of wasps belonging to different colonies from the same population are reported in Fig. 3. The modelled average faces (Fig. 3) give clues as to the elements of faces that might actually be used by wasps for colony recognition showing that the most differentiation is seen at the lower end of the brownish markings as well as in the overall top-to-bottom length of the brownish markings as explained above.

#### Discussion

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Our findings, for the first time, open the possibility that visual nestmate recognition in social wasps may not depend exclusively on individual recognition. We showed that, although each L. flavolineata female has a unique facial marking even within a colony, females belonging to the same colony resemble one another more than wasps belonging to different ones. Based on our analyses, within- and between-colony variation in the visual patterns is on a par with that in chemical profiles, suggesting that, similarly to CHCs, the wasp faces display adequate information for colony level recognition. Even though wasps' perception of their conspecifics' facial markings remains to be tested by behavioural experiments, these findings suggest that visual nestmate identification may rely on common facial features rather than, or in addition to, individual recognition. In the first case, each nest must have a unique signature shared by nestmates, while in the latter case, each individual must have a unique phenotype that has to be memorized.

While extracting common features from a category of visual patterns may be more cognitively demanding, individual recognition certainly requires more storage capacity. Indeed, the existence of a common visual cue by which most of the few nest members can be identified suggests that visual nestmate recognition might require a memory of just one average defining feature (a colony label), as occurs when they memorize the colony odour (Bos and d'Ettorre 2012). We do not yet know what features the wasps might use in category formation, but the average facial markings as well as other

**Cuticular Hydrocarbons** 



Exp. Var. 43.8 %

Fig. 2 Plot of the scores of the two first discriminant functions obtained by the discriminant analysis using facial markings (*left*) or chemical profiles (*right*) belonging to 12 colonies. *X-axis* and *Y-axis* represent the explained variance by the first and second function, respectively. Each *open circle* represents a female wasp. In each plot, different colours indicate different colonies. *Black squares* are the centroids (i.e. the mean value for each colony). Each *ellipsoid* encloses all the wasps

belonging to the same colony. The size of the ellipsoids is indicative of the within-colony variation in facial markings (*left*) and odours (*right*), while their superimposition rate indicates the between-colony variation, so that smaller and less overlapped ellipsoids correspond to colonies with lower and higher within- and between-colony variation, respectively. The colony-specific variation in facial patterns is on a par with that observed for odours



Fig. 3 Modelled average facial markings obtained from the real face images of females belonging to three different colonies

elements like spatial frequency or amount of contrast might be all suitable candidates. A similar mechanism based on visual category formation might also occur in *P. fuscatus* (i.e. the only other species of wasp that are known to use faces for individual/nestmate recognition) even though, in this case, the different parts of the faces vary in colouration and do not display any dots or shapes (Tibbetts 2002).

Individual and class level recognition do not exclude each other and the same facial cues may be used for multiple levels of recognition. Our analysis left 25 % of the total variance of the facial marking in our sample unexplained, indicating that many aspects of the shape of the facial markings varied across individuals. Thus, facial markings are clearly unique and they may inform the viewer about both colony membership and individual identity. Behavioural experiments that manipulated the facial signals of L. flavolineata already provided conclusive proof of the effectiveness on information transfer by individual facial markings (Baracchi et al. 2013, 2015). Previous field experiments showed that resident wasps responded aggressively towards nestmates whose facial markings were experimentally altered, either by slightly enlarging or reducing the brownish facial marking using brown or vellow paint, respectively (Baracchi et al. 2012). Our new data open the possibility for the existence of group level visual recognition. The percentage of correct assignment as nestmates and non-nestmates obtained in our discriminant analyses was only about 60 % either using odours or facial markings. Even though this percentage can vary depending on the relative number of variables entered in the analysis, it agrees with the findings that nestmate recognition system of L. flavolineata is far from perfect. Indeed, when visual cues or chemical cues were experimentally presented in isolation in field tests, this caused erroneous responses towards alien females in 31 and 45 % of cases, respectively (Baracchi et al. 2015).

The similarities in the facial markings of nestmates suggest a genetic basis and the heritability of these clypeal traits. In *L. flavolineata*, similarly to most primitively eusocial species, the colony is started by a single female and other related or unrelated females can occasionally join the new foundation (Samuel 1987). Moreover, young females can leave the natal nest soon after eclosion and it has been suggested that those individuals could be not the daughters of the dominant females but rather of a previous one (Samuel 1987). Larval development is relatively long in this species (about 110 days) and sometimes dominant females die long before daughters' emergence (Samuel 1987). An early study settled on an intracolony female relatedness as rather moderate (i.e. 0.22; because of the haplodiploid sex-determination system, 0.75 would be the value if all the females were fully sisters) using allozymes (Strassmann et al. 1994). However, more recent and reliable analyses based on DNA microsatellite markers provided much higher values of relatedness (i.e. 0.52 and 0.56 (Sumner et al. 2002), 0.45 (Sumner 1999) and 0.46 (Bridge 2005)). Hence, it is reasonable to conclude that many colony members are actually relatives and that the face resemblance among nestmates is most likely linked to their kinship. as it has been suggested for the visual quality signal in P. dominula (Tibbetts 2010).

While our finding showed a correlation between facial patterns we measured and colony membership, this does not prove that wasps are able to perceive and rely on these colony similarities. The occurrence of face discrimination at the colony level remains to be tested in the field. For instance, wasp colonies might be presented either with alien females with increasingly dissimilar facial features from those of resident wasps or with artificial face stimuli that are members of the group cluster but are individually different to all other faces on a nest, similar to the experiments performed by Baracchi and co-workers (Baracchi et al. 2013). Intruders with faces more similar to those of their hosts might have more chances of being erroneously adopted by colonies than females with more dissimilar faces. In L. flavolineata, young unrelated individuals occasionally join alien colonies (Coster-Longman et al. 2002) and females looking for a new colony where to settle on might find it by a trial-and-error approach. The existence of a visual nestmate recognition rather than, or in addition to, an individual recognition would provide us with the opportunity to delineate pros and cons of different recognition systems and their implications for group living organisms.

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