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Visual Signals of Individual Quality in a European Solitary Founding Paper Wasp

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Abstract

Conventional signals are maintained via social costs and commonly used in the animal kingdom to assess conspecifics' agonistic ability during disputes over resources. In the last decade, some experimental studies reported the existence of visual conventional signals in several social wasp species, being good rank predictors in different social contexts. Females of the social wasp *Polistes gallicus* do not cooperate to start nests but they often try to usurp conspecific nests. Here, we showed that the reproductive females of this species have variable facial colour patterns that function as conventional signals. Wasps with larger black spots on their clypeus are more likely to successfully overwinter, are larger, and are better at fighting and at holding a nest. Furthermore, in field experiments, resident foundresses rely on facial pattern to assess usurpers' fighting abilities, modulating their defence reaction accordingly, so that rivals with larger black spot receive more aggression than rivals with smaller or no black spots on the clypeus. Our study reveals that visual recognition abilities are widespread among paper wasps that, regardless of their social biology, face similar selective pressures within competitive contexts.

Introduction

Competition over limited resources leads to costly social interactions. Many animals deal with that by assessing rivals' competitive abilities before engaging in aggressive contests. By estimating the strength of rivals, an individual can avoid costs related to an escalated contest with stronger or more motivated rivals (Maynard Smith & Harper 2003; Searcy & Nowicki 2005). Assessment can be based on signals that are obviously associated with a bearer's competitive abilities (Parker 1974; Hurd 2006), like antlers (Barrette & Vandal 1990). On the other hand, assessment can be based on signals devoid of clear physical or physiological link with its bearer's competitive abilities (conventional signals: Guilford & Dawkins 1995; Searcy & Nowicki 2005). For example, the visual facial pattern of some eusocial and primitively eusocial wasps is a conventional signal of fighting ability (Tannure-Nascimento et al. 2008; Tibbetts & Lindsay 2008; Tibbetts & Sheehan 2011; Baracchi et al. 2012).

If there is no required link between signal phenotype and the information conveyed, how conventional signals can accurately inform about individual's ability (Whitfield 1987)? In other words, how can they be honest? Some conventional signals are thought to be accurate because there are costs associated with the production of the signal itself. For example, house finches cannot synthesize the carotenoid pigment that colours their chest *de novo*. As a result, foraging for carotenoid rich food is thought to be the cost that ensures the accuracy of the house finch chest patch (Hill 1991). Conversely, some conventional signals lack obvious production costs (Senar 2006), as the black facial spots on *Polistes dominula* wasps (Tibbetts & Dale 2004). In this case, accuracy is thought to be maintained by social costs (Tibbetts & Izzo 2010) or by ontogenetic mechanisms that reliably link the development of a signal with its bearer's quality (Tibbetts & Izzo 2010).

Polistes gallicus is a common circum-Mediterranean paper wasp. Its colonies are started by a solitary female that builds the nest in open locations (Cervo & Turillazzi 1989). During the pre-worker emergence period, around 90% of nests are preyed by birds and foundresses who lost their nests often try to usurp conspecific nests (Dani & Cervo 1992). At this time of the season, encounters and aggressive interactions among competing unfamiliar individuals become thus very common. Under this scenario, class-level recognition (such as quality signals or 'badges of status') is expected to evolve (Rohwer 1982; Shreeve 1987; Zulandt Schneider et al. 1999). *Polistes gallicus* females have a variable facial pattern that is a good candidate for a conventional quality signal. Individuals may have a totally yellow clypeus or they can have a single rounded black spot of variable size (Fig. 1). The variable facial pattern in *P. gallicus* resembles that of other paper wasps in which it is considered as functioning as a visual conventional signal. Here, we test whether the black spot on the clypeus of *P. gallicus* foundresses is associated with several aspects linked to individual's quality such as (1) the probability to successfully overwinter, (2) body size, (3) fighting ability and (4) the ability to hold a nest. We then test whether foundressess rely on rivals' black spots to evaluate conspecifics' strength.

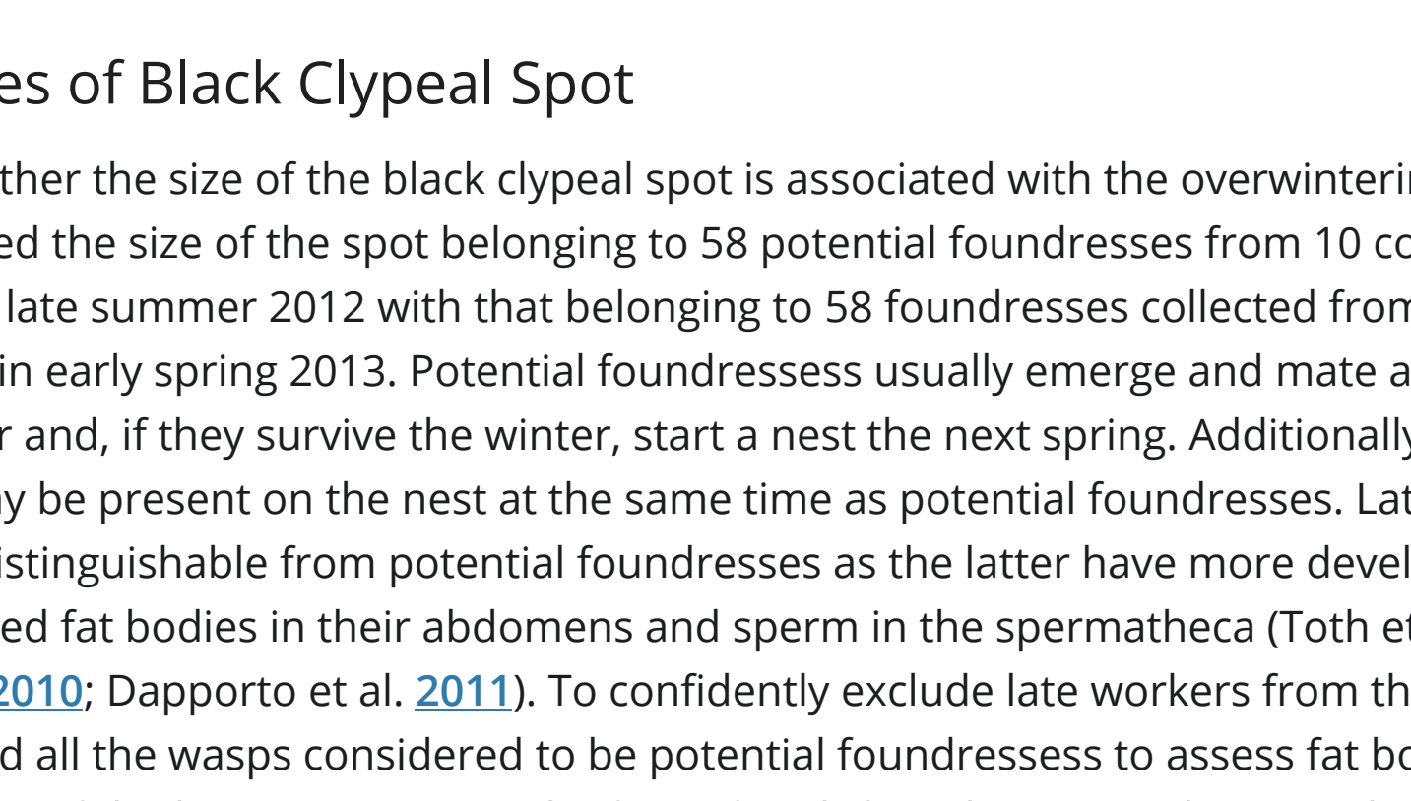

Figure 1 Open in figure viewer | PowerPoint

Portraits showing the natural variability of the black spot size on the *Polistes gallicus* females clypeus.

Methods

Wasp Collection and Study Place

Polistes gallicus reproductive females were collected in the field, next to Peretola airport, Florence (Tuscany) during early springs in 2012 and 2014 and late summer in 2012. When necessary, wasps were killed by freezing.

Correlates of Black Clypeal Spot

To test whether the size of the black clypeal spot is associated with the overwintering success, we compared the size of the spot belonging to 58 potential foundresses from 10 colonies collected in late summer 2012 with that belonging to 58 foundresses collected from the same population in early spring 2013. Potential foundressess usually emerge and mate at the end of the summer and, if they survive the winter, start a nest the next spring. Additionally, late workers may be present on the nest at the same time as potential foundresses. Late workers are easily distinguishable from potential foundresses as the latter have more developed and multistratified fat bodies in their abdomens and sperm in the spermatheca (Toth et al. 2009; Hunt et al. 2010; Dapporto et al. 2011). To confidently exclude late workers from the sample, we dissected all the wasps considered to be potential foundressess to assess fat bodies and (only in cases of doubt) insemination. The face of each foundress was photographed with a digital camera connected to an optical microscope, and the spot size and the maximum head width were measured (and reported in pixels) using the software Image-J (available on line at http://rsbweb.nih.gov.proxy.lib.fsu.edu/ij/). Head width is commonly used as an estimate of body size in *Polistes* (Haggard & Gamboa 1980; Dani 1994; Tibbetts & Dale 2004; Cervo et al. 2008; Ortolani & Cervo 2010).

To test whether the spot size is associated with fighting ability and ability to hold a nest, we promoted dyadic encounters among 27 pairs of foundresses in early spring 2014, under laboratory conditions. Each pair of wasps was previously matched by body mass and then was allowed to interact in a plastic cup of 0.15 l for 30 min. Inside each cup, there was an alien pre-emergence nest containing some eggs and larvae. The interactions were video recorded and an observer blind to the predictions registered frequency and direction of aggressive behaviours and the time each wasp spent on the nest. The foundressess in each pair came from two different localities at least 1 km apart to reduce the possibility they had met before. Wasps were removed from their own pre-emergence nests and kept in plastic cups provided with sugar and water one day before the experiment. They were killed for clypeal black spot analysis after the experiment. In each pair, the most aggressive wasp was considered to have more fighting ability (dominant) than the respective partner (subordinate). Similarly, the wasp that spent more time on the nest was considered to have more ability to hold a nest than the respective partner.

Do Wasps Rely on the Black Spot on the Clypeus?

We tested whether the receiver's aggressive response is associated with senders' facial visual pattern. In early spring 2013, each one of the 48 focal foundressess (receivers) was introduced to two dead conspecific foundresses (senders) that differed in the facial visual pattern (one with and the other without a natural black spot on the clypeus). We used five pairs of senders collected more than 5 km apart from the place where we collected the focal wasps to reduce the possibility they had met before. The pairs of senders were previously matched by head width and rinsed in 500 μl of pentane for 24 h to remove any chemical cue (cuticular hydrocarbons).

We also tested whether the size and the shape of the spot on sender's clypeus affect the receiver's aggressive response. Using a new set of early spring foundresses, we introduced to the 42 focal wasps (receivers) four pictures of a female face (senders) with four artificially increased levels of black spot on the clypeus (0%, 3%, 12% and 50% of the total area of the clypeus). Furthermore, in another set of early spring foundresses, we introduced to 30 additional focal wasps (receivers) two pictures of the same female face (senders) with the same black spot area but different in shape – a circle and a six pointed star. In both experiments, pictures showed faces reproduced at natural size, 3 mm, which is the average head width of *P. gallicus* queens belonging to the studied population. In each picture, the size of the black spot on the wasp face was manipulated with the software Photoshop CS, version 8.0.1 (Adobe Systems Incorporated 1990-2003, San Jose, CA, USA).

All the three experiments were carried out in the field. Each focal wasp was tested on its pre-emergence nest and used only once. Each sender was individually fixed on the tip of a 15-cm long iron stick (dead wasps were fixed by the thorax while pictures were fixed by the opposite side of the one containing the wasp face). Each sender was presented in a random order to each focal wasp for 30 s. The presentation interval between two senders was 30 min. The behaviour of focal wasps was videotaped, and then, an observer blind to the predictions computed the latency of attack (seconds elapsed until the first bite) and the number of bites displayed by focal wasps towards each sender.

Statistical Analyses

To test the association among black facial pattern, overwintering success and body size, we ran a generalized linear model (GLZ) in which spot size was entered as dependent variable, foundress group (potential foundresses vs. spring foundresses) was entered as factor and head width as covariate. To test for any association between facial patterns and fighting ability, we ran a GLZ for a binomial response in which whether or not a female was dominant was entered as dependent variable, while spot size and head width were entered as covariates. We also ran a GLZ for a binomial response to test how facial pattern is associated with nest holding potential. Whether or not a female was the holder of a nest was entered as the dependent variable while spot size and head width were entered as covariates and dominance status was entered as a factor. Foundress' response towards dead wasps with and without black spot on the clypeus was compared using Wilcoxon signed-rank test. Foundresses' response towards female face pictures with different black spot sizes was compared using ANOVA repeated measures design after variables have been log-transformed. As the data and homogeneity of variances and sphericity could not be assumed in several cases, we performed corrections according to Huynh-Feldt epsilon. Finally, receivers' response towards female pictures with different black spot shape was compared using Wilcoxon signed-rank test. All analyses were performed using the Statistical program SPSS® 13.0 for Windows® (Apache Software Foundation, Wilmington, DE, USA).

Results

Correlates of Black Spot Size on the Clypeus

Spring foundresses have bigger black spot than potential foundresses (Fig. 2) ($\chi^2 = 7.257$, N = 116, p = 0.007), and bigger heads are associated with bigger black spots (Fig. 3) ($\chi^2 = 55.492$, N = 116, p < 0.0001). Whether or not a foundress was dominant was associated with the spot size ($\chi^2 = 4.011$, N = 42, p = 0.042) but not with the head width ($\chi^2 = 2.958$, N = 42, p = 0.085). Thus, independent of head width, dominant foundresses have bigger spot than subordinate ones (Fig. 4). Finally, whether or not a foundress stands out as a nest holder was associated with the size of the black spot ($\chi^2 = 4.575$, N = 42, p = 0.032) with the dominance status ($\chi^2 = 13.666$, N = 42, p = 0.001) but not with the head width ($\chi^2 = 0.009$, N = 42, p = 0.923). Thus, wasps that are dominant and have bigger spot on the clypeus are likely to be the nest holders (Fig. 5).

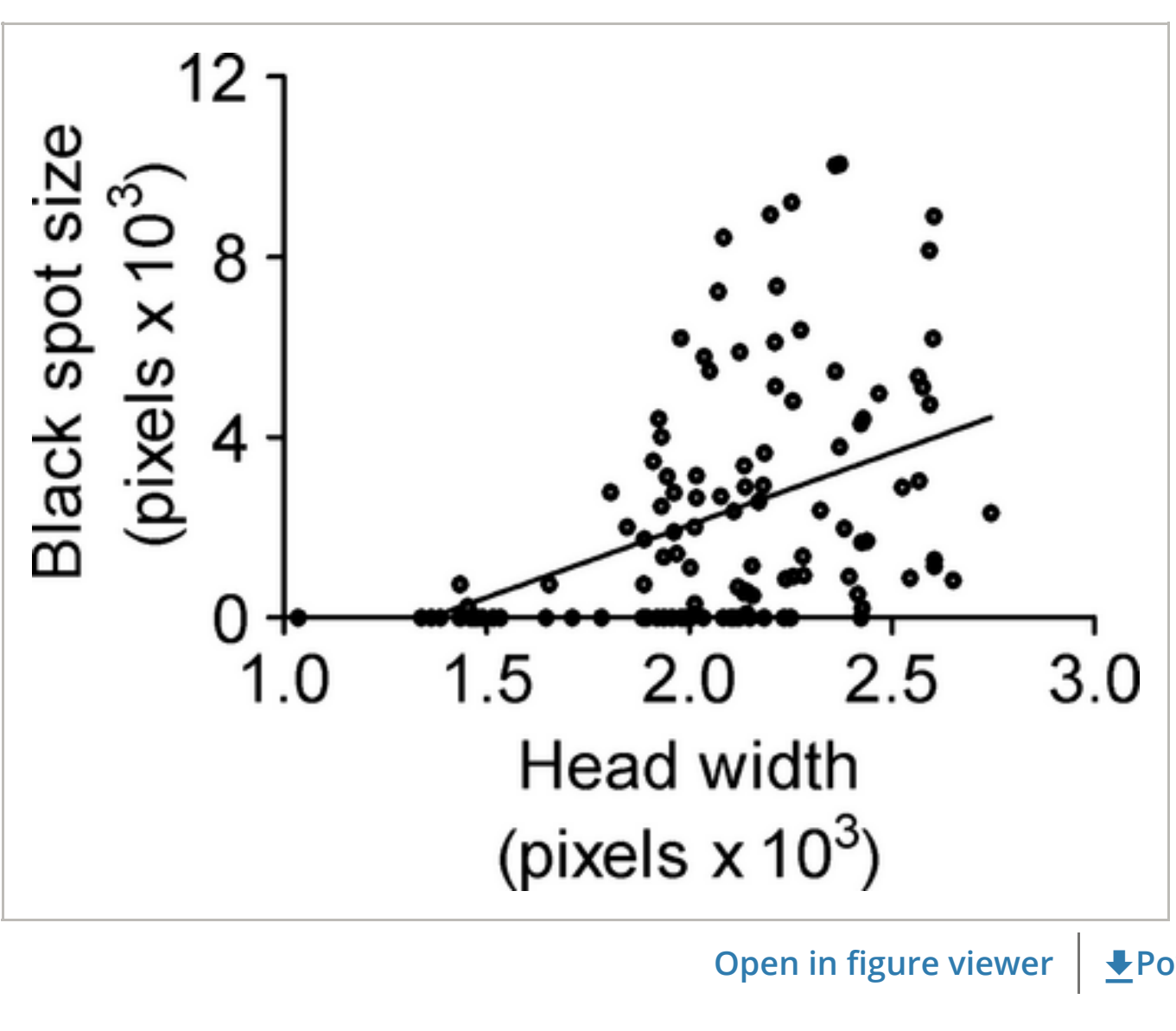

Figure 2 Open in figure viewer | PowerPoint

Black spot size in potential and spring foundresses. Box plots show medians, 25th and 75th percentiles and whiskers are minimum and maximum values. Different letters mean statistical differences between groups.

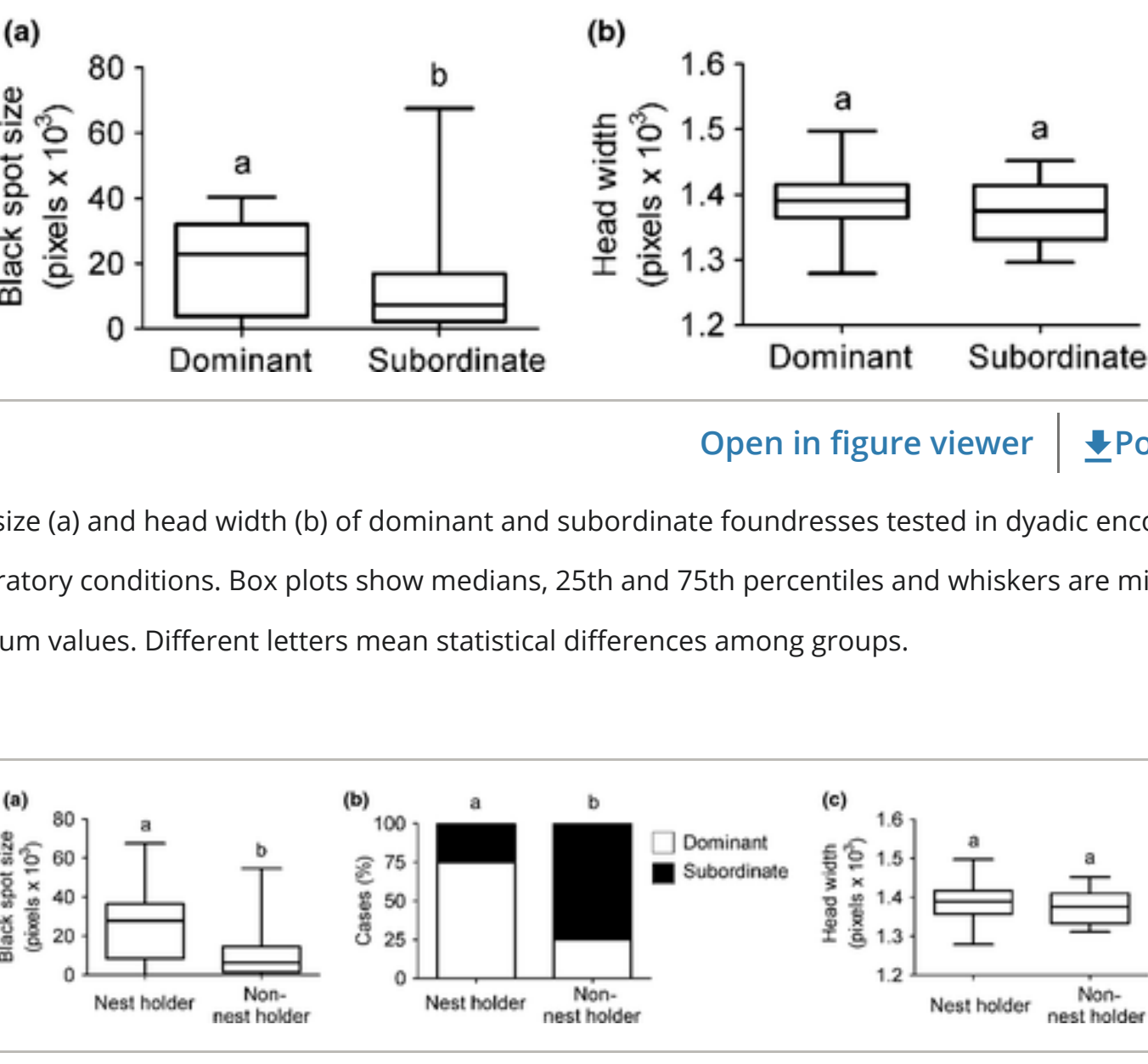

Figure 3 Open in figure viewer | PowerPoint

Relationship between head width and black spot size in reproductive females.

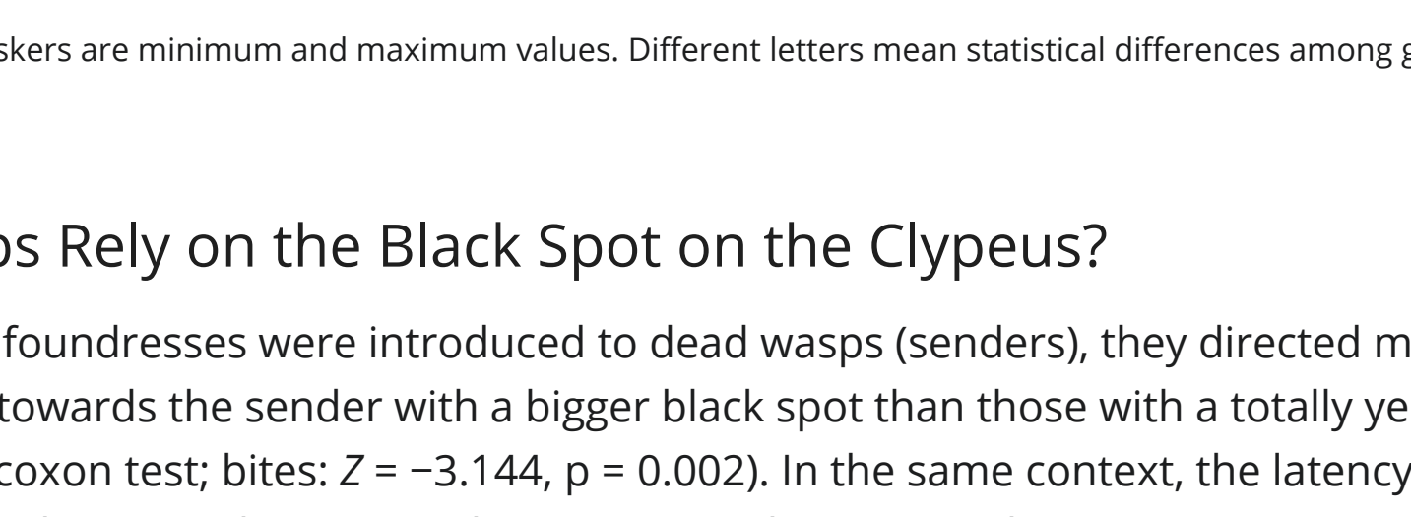

Figure 4 Open in figure viewer | PowerPoint

Black spot size (a) and head width (b) of dominant and subordinate foundresses tested in dyadic encounters under laboratory conditions. Box plots show medians, 25th and 75th percentiles and whiskers are minimum and maximum values. Different letters mean statistical differences among groups.

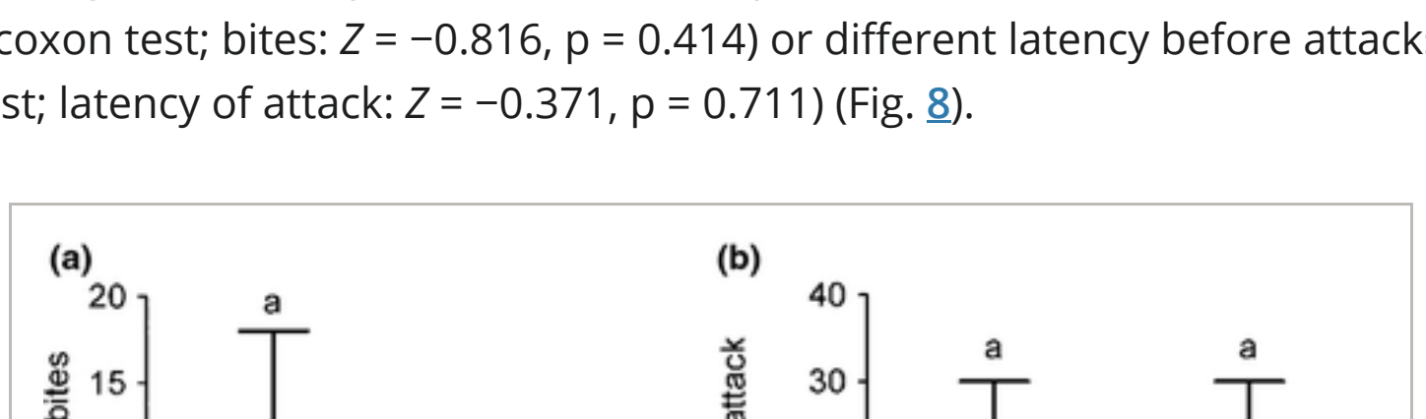

Figure 5 Open in figure viewer | PowerPoint

Black spot size (a), dominance status (b) and head width (c) of foundresses according to their nest hold status tested in dyadic encounters under laboratory conditions. Box plots show medians, 25th and 75th percentiles and whiskers are minimum and maximum values. Different letters mean statistical differences among groups.

Do Wasps Rely on the Black Spot on the Clypeus?

When focal foundresses were introduced to dead wasps (senders), they directed more aggression towards the sender with a bigger black spot than those with a totally yellow clypeus (N = 48; Wilcoxon test; bites: $Z = -3.144$, p = 0.002). In the same context, the latency of attack did not differ between the two senders (N = 48; Wilcoxon test; bites: $Z = -0.950$, p = 0.342) (Fig. 6). The behaviour of the focal foundresses towards pictures (senders) with different black spot size was statistically different so that increasing black spot size on sender's face resulted in increased aggressiveness (ANOVA repeated measures, N = 42: F3 = 2.694, p = 0.049) and reduced latency to attack (ANOVA for repeated measures, N = 42: F3 = 2.968, p = 0.035) (Fig. 7). Pictures showing faces with spots of different shapes did not elicited different number of bites (N = 30; Wilcoxon test; bites: $Z = -0.816$, p = 0.414) or different latency before attacks (N = 30; Wilcoxon test; latency of attack: $Z = -0.371$, p = 0.711) (Fig. 8).

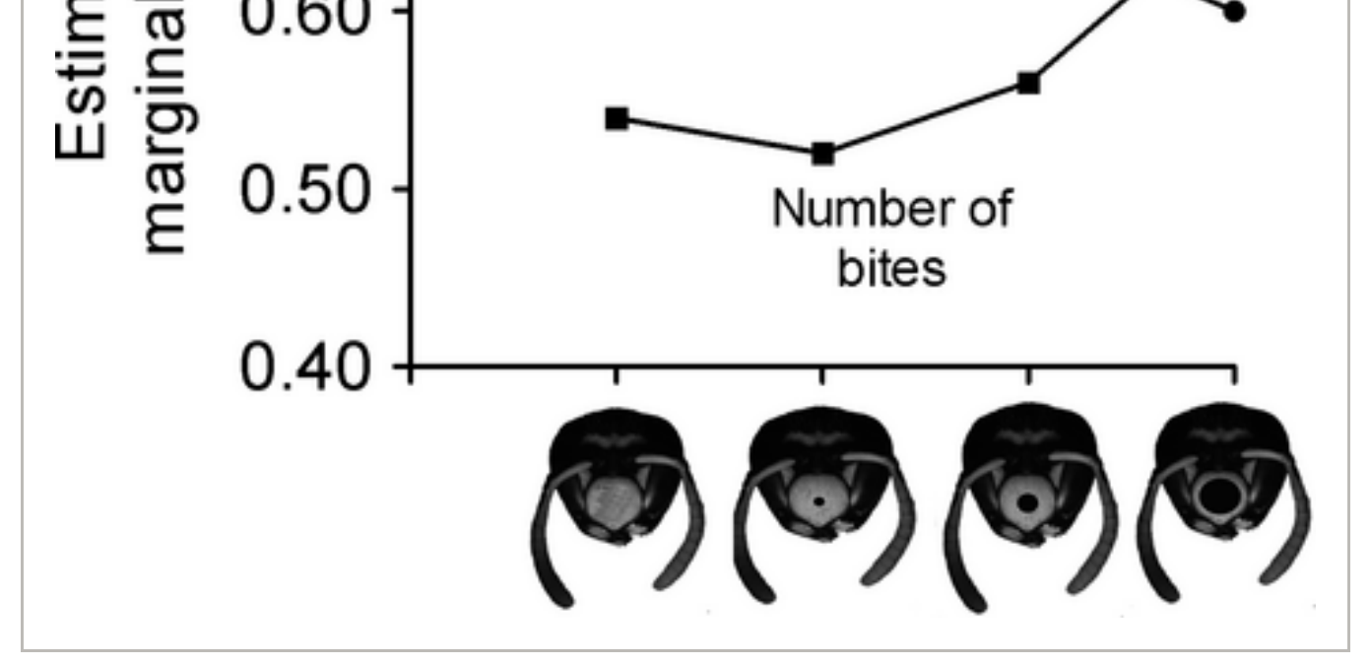

Figure 6 Open in figure viewer | PowerPoint

Number of bites (a) and latency of attack (b) displayed by resident wasps towards senders with and without a black spot on the clypeus. Box plots show medians, 25th and 75th percentiles and whiskers are minimum and maximum values. Different letters mean statistical differences among groups.

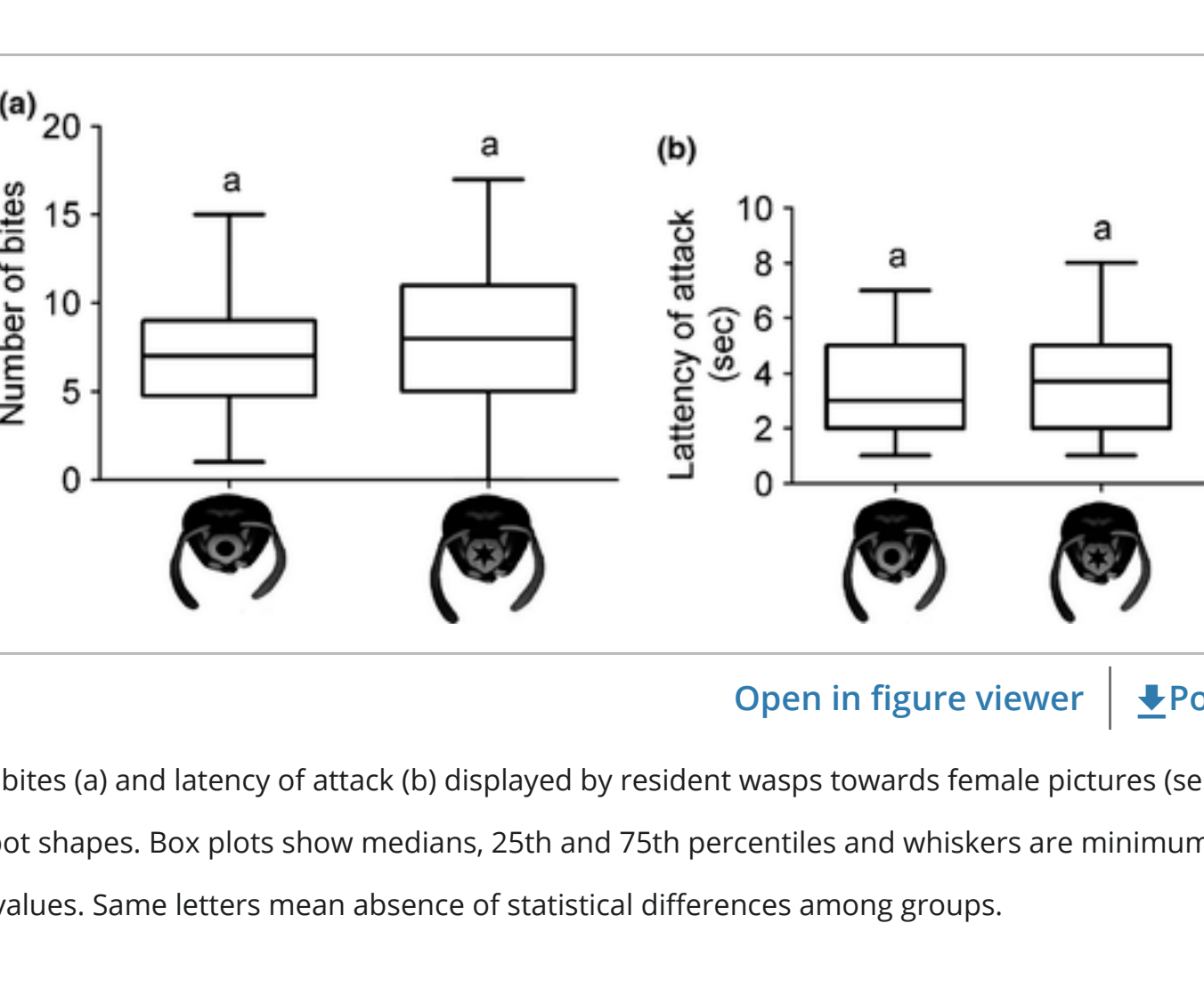

Figure 7 Open in figure viewer | PowerPoint

Number of bites and latency of attack displayed by resident wasps towards female pictures (senders) with four experimentally altered black spot size. Box plots show medians, 25th and 75th percentiles and whiskers are minimum and maximum values.

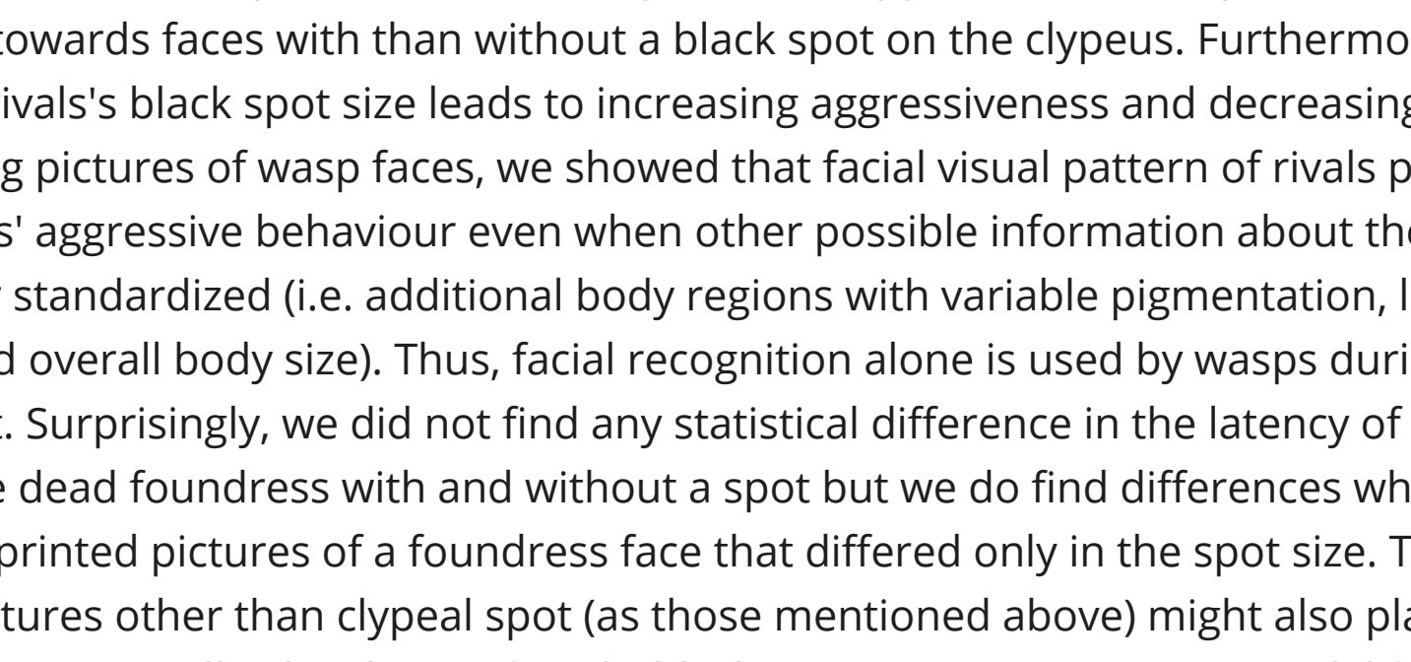

Figure 8 Open in figure viewer | PowerPoint

Number of bites (a) and latency of attack (b) displayed by resident wasps towards female pictures (senders) with different spot shapes. Box plots show medians, 25th and 75th percentiles and whiskers are minimum and maximum values. Same letters mean absence of statistical differences among groups.

Discussion

Polistes gallicus reproductive females have variable facial colour patterns that function as conventional quality signals. Wasps with larger black spots on the clypeus are also larger in body size, more likely to overwinter, better at fighting and at holding a nest. Foundresses' aggressive behaviour depends on the facial pattern of opponents, as wasps are more aggressive towards faces with than without a black spot on the clypeus. Furthermore, increasing rivals's black spot size leads to increasing aggressiveness and decreasing latency to attack. Using pictures of wasp faces, we showed that facial visual pattern of rivals predicts foundresses' aggressive behaviour even when other possible information about the rival was removed or standardized (i.e. additional body regions with variable pigmentation, limbs position and overall body size). Thus, facial recognition alone is used by wasps during rival assessment. Surprisingly, we did not find any statistical difference in the latency of attack towards the dead foundress with and without a spot but we do find differences when presenting printed pictures of a foundress face that differed only in the spot size. This points out that features other than clypeal spot (as those mentioned above) might also play a role in rival assessment. Finally, the shape of rival's black spot is not important to model foundress' aggressive behaviour, as foundressess were equally aggressive towards two female face pictures differing only in spot shape.

Fighting abilities and the ability to hold a nest were associated with foundress' facial pattern but not with foundress' body size. Thus, although associated, head width and foundress' spot size may provide different information about a rival's competitive ability.

Many signals lack obvious production costs (Senar 2006). For example, black spots on the clypeus of North America invasive populations of *P. dominula* wasps account for <1% of the total black pigment on a wasp body (Tibbetts & Dale 2004). This seems to be also the case in *P. gallicus* (authors' pers. obs.). Thus, a low-quality foundress could cheat by producing a high-quality signal (bigger black spot), winning more fights and being more likely to hold a nest. Our results suggest that, similar to the North America population of *P. dominula* (Tibbetts & Dale 2004), the signal honesty may be achieved by social costs. Indeed, bigger spotted senders receive more aggression than small spotted ones. Thus, despite of the quality information conveyed by the spot, females might potentially evaluate whether the signal matches sender's agonistic ability, so that just individuals with high competitive abilities could bear a facial pattern associated with high individual quality. This is actually what occurs in *P. dominula*, where a mismatch among signal and behaviour produces costly social interactions (Tibbetts & Izzo 2010).

The finding that big spotted *P. gallicus* foundresses are better competitors than small spotted ones, even though both of them are present in a natural population, rises a question about the mechanism maintaining signal variability. In *P. dominula*, signal variability is maintained because it is condition dependent (Tibbetts & Izzo 2010). In this case, well-nourished larvae develop into adults with a high-quality kind of facial pattern while less nourished larvae develop into adults with low-quality kind of facial pattern (Tibbetts & Izzo 2010). A similar mechanism might maintain signal variability in *P. gallicus*. Successfully overwintering often depends on lipid stores and body size (Strassmann 1985), so that well-nourished reproductive wasps are more likely to survive the winter than less nourished ones. Since *P. gallicus* foundresses with bigger spot are also more probable to survive the winter, it is possible that big spotted foundresses, that we know to be larger than small spotted ones, also have higher levels of lipid stores. Thus, spot development could be linked to the nutritional state of individuals.

The frequent usurpation attempts faced by *P. gallicus* foundresses (Dani & Cervo 1992) fit the scenario in which class-level recognition (like quality signals or 'badges of status') is expected to evolve (Rohwer 1982; Shreeve 1987; Zulandt Schneider et al. 1999): frequent interactions among competing unfamiliar individuals with quick and inexpensive shift systems (i.e. flight). We suggest that the black spot size on foundress clypeus might be useful for foundresses to assess rivals quality during usurpation. The occurrence of visual conventional signals mediating the interactions among potential usurpers and residents is also reported for *P. dominula* (Tibbetts & Shorter 2009). In this species usurpers whose facial pattern is associated with high quality are more likely to usurp a nest from a resident foundress than usurpers whose facial pattern is associated with low quality. Furthermore, residents whose facial pattern is associated with high quality are more likely to resist against usurpation attempts than residents whose facial pattern is associated with low quality (Tibbetts & Shorter 2009).

Quality signals are expected to be particularly relevant when a social competition among numerous unfamiliar rivals exists (Rohwer 1982). In paper wasps, this scenario occurs when, for example, foundresses try to usurp or join an alien nest. In *P. gallicus,* however, foundresses are not likely to join. As a consequence, for the first time, we provide evidence that nest usurpation context alone may promote the evolution of quality signals. Nest usurpation attempts are quite common in *Polistes* (Gamboa 1978; Dani & Cervo 1992; Gamboa et al. 2004). It is an important selective force in paper wasps, as usurped nests are commonly found, and usurpation fights can be fatal (Field 1992; Cervo 2006). Quality signals may allow rivals to quickly assess each other's agonistic abilities without engaging in intense competition (Maynard Smith & Harper 2003; Searcy & Nowicki 2005). Nest usurpation is also observed in most of the independent colony founding eusocial Hymenoptera, in many solitary Hymenoptera (Field 1992) and in many other social species (Brockmann 2001), and future investigations in all these species subject to high rates of usurpation might provide new insights for the evolution of quality signals.

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Literature Cited

Citing Literature

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