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# Badges of status in worker and gyne *Polistes dominulus* wasps

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Despite widespread interest in quality signals, a broad understanding of quality that incorporates information about signals used in a variety of contexts remains elusive. For example, relatively little is known about arbitrary signals of quality used during aggressive competition (badges of status). Recently, a new badge of status was found: black facial patterns in *Polistes dominulus* wasps. Previous work on *P. dominulus* facial patterns focused on queens, finding that facial patterns predict body size and social dominance. Here, I examine worker facial patterns for the first time. Worker facial patterns provide an interesting comparison with queens and help shed light on two unresolved issues: (1) Is there pre-imaginal caste bias in these primitively eusocial insects? (2) Is badge-of-status elaboration influenced by developmental environment? I show that worker and gyne (future queen) facial patterns are correlated with body size. Larger individuals have a larger proportion of their clypeus pigmented black, corroborating the relationship between body size and facial pattern found previously in queens. Independent of the size relationship, workers and gynes have different facial patterns. Gynes have the disrupted, black facial patterns that signal a high level of quality, while workers have yellow facial patterns associated with a low level of quality. The differences between worker and gyne facial patterns suggest that there is some pre-imaginal caste bias in these eusocial wasps. Workers and gynes are genetically similar but experience different developmental environments, so the differences between worker and gyne facial patterns suggests that badge development is influenced by environmental factors.

## Introduction

### Quality signaling and condition-dependence

Many ornamental features in animals are thought to signal quality. Generally, quality signals are cues that communicate information about aspects of their bearers' relative phenotypic and genetic constitution. There are many different aspects of quality: parenting ability, dominance, immune function, 'good genes', etc. (Zahavi 1975, Grafen 1990, Andersson 1994, Dale 2006). Despite keen interest in quality signals, our conceptualization of quality remains surprisingly limited. For example, we still know little about whether it is appropriate to unify the diverse range of signals referred to as 'quality signals' under a signal conceptual framework. Recently, there has been a push toward studying quality signal development, because understanding the factors that influence the development of different types of quality signals will help clarify the specific information conveyed by quality signals and the relationship between components of quality and total quality (Hunt *et al.* 2004).

Quality signals require high and differential costs to maintain the honest association between signaled and true quality (Zahavi 1975, Grafen 1990). Quality signals can be divided into two main groups based on their associated costs: sexual signals and badges of status. Signals used during inter-sexual mate choice (sexual signals) often have costs associated with signal development (production costs, Grafen 1990, Andersson 1994). Classic examples of sexual signals with production costs include long tails and carotenoid-based color patches (Hill 1991, Pryke *et al.* 2001). Signals used during agonistic competition between rivals (badges of status) are often hypothesized to have social costs associated with signal maintenance (Rohwer & Rohwer 1978, Tibbetts & Dale 2004). Badges are used in many contexts and taxa (review in Senar 1999, Pärt & Qvarnström 1997, Pryke & Andersson 2003, Tibbetts & Dale 2004), but the classic example is black throat patches used to settle minor dominance contests in flocks of birds (Rohwer 1975, Whitfield 1987, Senar 1999).

A key prediction of honest signaling models is that sexual signals with production costs should exhibit heightened condition-dependent expression (Grafen 1990). This prediction has been widely supported. In addition to a huge number of studies that correlate condition with sexual signal elaboration (reviews in Andersson 1994, Johnstone 1995), there are a number of carefully-designed studies that have used environmental manipulation during development to show that handicap traits are more condition-dependent than neutral traits (reviewed in Cotton *et al.* 2004).

Badges are not thought to impose production costs, so heightened condition dependence is not a key prediction of badge-of-status models (Maynard-Smith & Harper 1988, Owens & Hartley 1991, Johnstone & Norris 1993). Consequently, condition-dependence is sometimes used as a simple method of discriminating between badges and sexual signals; sexual signal development is thought to be influenced by the environment, while badge development is not (Gonzalez *et al.* 1999, McGraw *et al.* 2002, Senar *et al.* 2003). However, other studies suggest that the distinction may not be that simple. Veiga and Puerta (1996) found that juvenile nutrition may influence badge size. Further, Griffith *et al.* (1999) used a brood swap experiment to show that the size of the social father's badge, not the genetic father's badge, is correlated with offspring badge size, suggesting that environment plays a stronger role in badge development than genotype. Clearly, more research is needed to test the influence of developmental environment on adult badge quality.

## Background on *Polistes dominulus* wasps

In the early spring, *P. dominulus* paper wasp nests are started by one or multiple overwintered, nest-founding females (foundresses). In multiple-foundress colonies, foundresses form a linear dominance hierarchy that determines the amount of reproduction, work, food, and aggression each foundress receives (Pardi 1942, West-Eberhard 1969, Noonan 1981, Reeve 1991). At nest-founding, foundresses fight vigorously to establish dominance ranks. As the season progresses, dominance interactions become highly ritualized, with subordinates immediately submitting to dominants. After workers emerge from pupation, they incorporate themselves into the linear dominance hierarchy, although workers are subordinate to all foundresses and generally do not reproduce (reviews in Röseler 1991, Reeve 1991). Workers spend most of their time working on the nest, though some workers leave the parental colony to start their own nest (Reeve *et al.* 1998). Later broods of offspring are composed of gynes (potential queens) and males. Workers and gynes are primarily distinguished by emergence date, as they appear morphologically identical and both can reproduce (Solis & Strassmann 1990, Mead *et al.* 1995, Field & Foster 1999). Gynes typically experience a more favorable developmental environment than workers (Hunt & Amdam 2005), but gynes do not require specialized rearing conditions, like the royal jelly required for honeybee queen production (Seeley 1996). Gynes enter diapause in late fall then start their own nests the following spring (Reeve 1991).

*Polistes dominulus* paper wasps are covered in yellow and black patterns that are stable and fixed for life. Although most of these patterns are identical from wasp to wasp, there is extensive variation in the size, shape, and number of black spots on the face (clypeus) of female *P. dominulus* (Tibbetts & Dale 2004). Female clypeus patterns are a badge-of-status among foundresses. Clypeus patterns are associated with size; larger females have a higher proportion of their clypeus pigmented black and have more ‘disrupted’ (wavy and spotted) patterns. Independent of size, facial patterns are associated with dominance. More dominant females have larger, more disrupted black spots on their face (Tibbetts & Dale 2004).

The badge-of-status system in wasps is parallel to badges-of-status in other animals, as it appears to be a variable, visible, arbitrary, melanin-based signal of size and dominance (Tibbetts & Dale 2004). However, the badge-of-status system in wasps is different in one key way. Wasps are social insects, so they have multiple broods of offspring over the year. Early and late emerging broods do not differ systematically with respect to genotype, but late emerging offspring typically experience higher food availability than early emerging offspring (Hunt & Amdam 2005). I take advantage of this natural environmental variation to test how badges are influenced by developmental environment. I predict that late-emerging wasps (gynes) should have larger, more broken black facial spots than earlier emerging wasps (workers).

Here, I examine the facial patterns of workers and gynes for the first time. I test whether offspring that emerge at different times of the colony cycle have different facial features. If later emerging offspring have higher quality facial patterns than earlier emerging offspring, badge development is likely influenced by environmental factors. If early and late emerging offspring have similar facial patterns, badge development is likely not influenced by environmental factors. In addition, I test whether offspring facial patterns are associated with body size. A positive relationship between body size and facial patterns supports the relationship found previously in foundresses (Tibbetts & Dale 2004).

## Methods

### Worker and gyne facial patterns 2002

*Polistes dominulus* are a paper wasp species native to Europe that have recently become extremely common in the US (Johnson & Starks 2004). In 2002, I obtained simple estimates of worker and gyne facial patterns by recording offspring facial patterns on 7 single-foundress *P. dominulus* nests in Ithaca, NY, at the beginning and end of the colony cycle. Nests were assessed on 4 July (approximately 2 weeks after first worker emergence) and 4 August (at gyne emergence). Because an individual wasp’s face does not change over time (personal observation), this sampling procedure assesses how nest composition changes as new wasps emerge and old wasps die. Nests were sampled at dawn, when all colony members are present. On each date, I categorized the facial pattern of every wasp on a nest (as described in facial categorization section). Mean nest tenure of workers in this population was 14 days (author’s own unpubl. data), so it is extremely unlikely that wasps were assessed during both sampling periods. All seven colonies had a single foundress who was marked and remained on the nest through the entire colony cycle. Hence, parentage of emerging offspring did not change over the colony cycle.

### Worker and gyne facial patterns 2004

Worker and gyne facial patterns were assessed in a more detailed manner by following *P. dominulus* nests in rural and semi-rural areas surrounding Ithaca, NY, over the entire season. Nests with queen usurpation were excluded from this study, so only nests where queen composition remained stable over the colony cycle were included in the analyses. Nests were censused early in the morning when all colony members were present and wasps were cool and inactive. Each nest was censused approximately once every five days. Because mean worker tenure is 14 days (author's own unpubl. data), censusing nests every 5 days allows a realistic assessment of emerging offspring. At each census, newly emerged wasps were individually marked with enamel paint, weighed with a balance accurate to 0.002 g, and their facial patterns were categorized as described below. Nests were followed from first worker emergence on 15 June until 24 August. Only nests where the dominant queen remained on the nest through the entire colony cycle were included in the analysis. In total, 622 offspring emerged from the nests. In 2004, Ithaca had the rainiest June, July, and August since 1879 (Eggleston 2004), so nests remained smaller than is typical (e.g. Tibbetts & Reeve 2003).

### Facial pattern categorization

The size and 'disruption' of wasp facial patterns was assessed by ranking wasps on a scale of 1–13. Wasps with larger, wavier, and more black spots received higher numbers on the index than wasps with smaller, smoother, and fewer spots. Therefore, facial patterns associated with the lowest level of quality received a 1 and facial patterns associated with the highest level of quality received a 13. These categorizations are a good way of getting basic information about wasp facial patterns without laborious image analysis. To test the reliability of the categorizations, I categorized 164 wasp faces using the 1–13 scoring method, then independently performed Adobe Photoshop image analysis on these same wasps. In Tibbetts and Dale (2004), Photoshop image analysis was used to assess two facial pattern parameters: (1) the proportion of the clypeus pigmented black, and (2) 'brokenness'. To calculate facial pattern brokenness, the area of the clypeus containing the population-wide badge variability was converted into a 30 × 60 pixel bitmap. Then, the number of pixels within each vertical column along the horizontal length of the clypeus was counted. Calculating the standard deviation of the vertical black pigment deposition in the central third of the clypeus provides the 'brokenness index'. The categorical rankings of facial patterns are significantly correlated with results of Photoshop analyses (facial pattern categorization versus computer analysis of proportion clypeus pigmented black $r^2 = 0.89$, $F = 1333.9$, $p < 0.0001$; facial pattern categorization versus computer analysis of 'broken-ness' $r^2 = 0.08$, $F = 13.37$, $p = 0.0003$). Therefore, the simple categorization provides a meaningful method of ranking facial pattern quality.

### Data analysis

Facial pattern scores were square-root transformed for normality. For 2002 data, I used a matched pair *t*-test to compare the mean facial patterns of wasps on a nest on 4 July (workers) with the mean facial patterns of wasps on that same nest on 4 August (gynes).

For 2004 data, I tested whether facial pattern varied with emergence date, weight, and their interaction, using a mixed model, two-way ANOVA. The factors were emergence date, weight, weight by emergence date interactions. The weight by emergence date interaction was not significantly associated with facial pattern, so it was removed from the final model. Nest was included as a random factor to control for any within nest similarity. The 2004 data were also analyzed a second time, including only those nests for where there was a single queen on the nest from nest foundation through the end of the colony cycle.

## Results

*2002*. Wasps on the nest at the beginning of the colony cycle (workers), had facial patterns with less black pigment and fewer black spots than later emerging wasps (gynes) ($t = 2.06$, $n = 7$, $p = 0.04$ (one tailed)). Given the small number of colonies, the results are not strongly significant, but do suggest that gynes had facial patterns that signaled a higher level of quality than did worker facial patterns.

*2004*. The facial patterns of offspring are significantly associated with date of emergence from pupation and body size (Table 1 and Fig. 1; whole model $r^2 = 0.44$, $n = 622$). Smaller wasps

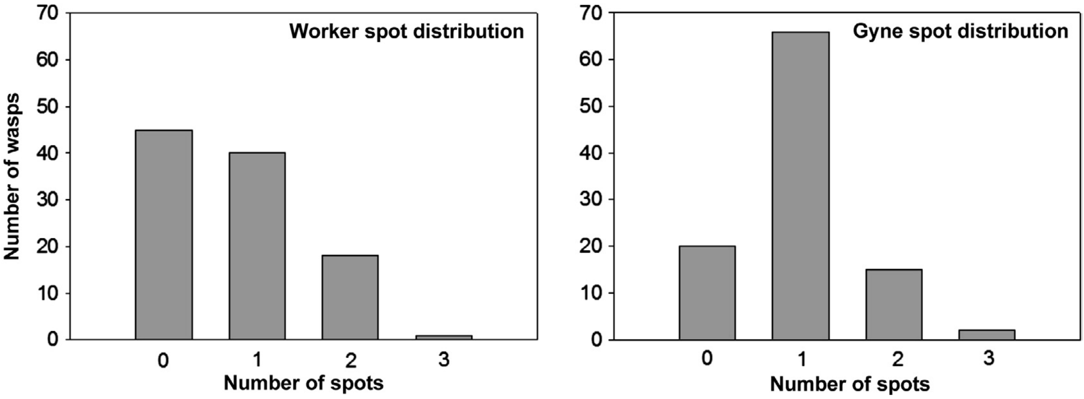

**Fig. 1.** Histogram showing the number of *Polistes dominulus* workers and gynes (potentially reproductive offspring) with 0, 1, 2, and 3 spots in 2004. Workers emerged from pupation before 1 July. Gynes emerged after 5 August. Data are pooled across all nests. Total 104 workers and 103 gynes.

had a smaller fraction of their face pigmented black and fewer black spots; larger wasps had blacker, more spotted clypeus patterns (Table 1). Independent of body size, facial patterns were also associated with emergence date; early emerging offspring had facial patterns associated with a lower level of quality, while later emerging offspring had facial patterns associated with a higher level of quality (Fig. 1). This analysis of 622 workers on 28 colonies includes single and multiple-foundress colonies, but no colonies where the original foundress was displaced by a usurper.

To ensure the presence of multiple foundresses on a nest did not influence the results, the same analysis was performed on a subset of 355 workers from 17 colonies. These 17 colonies had a single queen that remained alone with the nest throughout the entire colony cycle. Although the sample size is smaller, the results are similar to the analysis with all 28 colonies (whole model $r^2 = 0.43$; weight SS = 2.43, $F = 6.4$, $p = 0.012$; emergence date SS = 2.25, $F = 5.9$, $p = 0.015$).

## Discussion

### Badges of status and developmental environment

The facial patterns of newly emerged *P. dominulus* varied over the colony cycle. Late emerging offspring had larger, spottier black clypeus patterns than did early emerging offspring. Facial patterns were also associated with body size; larger wasps had facial patterns associated with a higher level of quality than smaller wasps.

The relationship between emergence date and facial pattern suggests that badge of status quality is influenced by environmental conditions during development. The only consistent difference between the development of *Polistes* gynes and workers is general rearing environment. Offspring genotype does not change in any predictable way over the colony cycle. Further, late emerging reproductive offspring don't receive specialized treatment, like the royal jelly and large nest cells used for honeybee queen production (Seeley 1996, O'Donnell 1998). Instead, general developmental environment changes over the colony cycle; later emerging offspring experience more favorable environmental conditions, including greater food availability (Hunt & Amdam 2005).

**Table 1.** Effect of emergence date and weight on offspring facial patterns in *P. dominulus* workers. Two-way ANOVA for offspring facial pattern, date of emergence from pupation, and wet body weight. Nest is included as a random factor. The weight by emergence date interaction was not significant, so it was removed from the model.

| Source of variation | d.f. | SS | *F* | *P* |
|---|---|---|---|---|
| Weight | 1 | 2.62 | 7.28 | 0.007 |
| Emergence date | 1 | 6.53 | 18.1 | < 0.0001 |

Badges-of-status are thought to reflect adult quality, so the relationship between badge phenotype and developmental environment is logical. Adult quality is thought to be influenced by developmental environment (review in Qvarnstrom & Price [2001]), so signals of quality should be influenced by environmental factors as well. Griffith *et al.* (1999) performed the one other study that examined the influence of early environment on adult badge development. They found a significant relationship between environmental factors and badge development; birds reared by higher quality social fathers developed bigger adult badges than birds reared by lower quality social fathers.

The significant relationship between developmental environment and badge elaboration seems at odds with a number of well-designed studies that found no relationship between environment and badge elaboration (Gonzalez *et al.* 1999, McGraw *et al.* 2002, Senar *et al.* 2003). However, the timing and type of the environmental stress is very different in these two sets of experiments. The studies that found no influence of environment on badge development imposed stressors in a brief window around the time that badges were developing. In contrast, Griffith *et al.* (1999) and our study looked at early development; both found that early environment influences badge quality. Therefore, physical environment can influence badge elaboration and the dichotomy between social and sexual signal development may not be as simple as previously thought. Clearly, experiments on environment and badge development are needed. Experiments where food quality and quantity are manipulated will be particularly useful to identify how the timing and severity of environmental stress influence signal development.

The positive relationship between offspring facial patterns and body size is consistent with the relationship found previously in foundresses (Tibbetts & Dale 2004). Interestingly, in both foundresses and workers, body size only predicts a portion of the variation in facial pattern. In foundresses, facial pattern is independently correlated with dominance. In workers, facial pattern is independently correlated with developmental environment. Therefore facial patterns provide information about multiple aspects of quality. Future research on the factors that influence quality signal development will provide more information about the specific information these signals convey.

## Facial patterns and pre-imaginal caste bias

The distribution of facial patterns in *P. dominulus* workers and gynes (future reproductives) also provides a window into paper wasp caste differentiation. The distributions of worker and gyne facial patterns overlap (Fig. 1), indicating that there are not discrete quality differences between workers and gynes. These results lend further support to previous studies that have found substantial morphological and behavior overlap between *Polistes* queens and workers (review in O'Donnell [1998]).

However, *P. dominulus* workers and gynes are not identical. Gyne facial patterns signal a higher level of quality than worker facial patterns. The quality difference between workers and gynes at pupal emergence indicates that components of quality are fixed during larval development. The influence of larval environment on adult caste has been a contentious issue. Some studies have found evidence for pre-imaginal caste biasing in primitively eusocial wasps (Gadagkar *et al.* 1990, Hunt 1991, Karsai & Hunt 2002). However, behavioral evidence indicates that workers can become queens under appropriate social and ecological conditions (Solis & Strassmann 1990, Mead *et al.* 1995, Field & Foster 1999). Our results suggest that aspects of quality are influenced by developmental environment such that individuals are more or less suited to becoming workers or queens at the moment of pupal emergence. However, workers and queens are not completely distinct. Changing ecology or social environment may change the costs and benefits of different strategies, offsetting an individual's pre-imaginal caste bias. Experiments in which development, ecology, and social environment are manipulated will help clarify the importance of these factors in determining caste fate.

This paper provides the first description and analysis of worker facial patterns in *P. dominulus* wasps. The badges-of-status in *P. domi-*

*nulus* allow us to address basic questions about quality signaling and pre-imaginal caste bias. *Polistes* have been a valuable model system for behavioral and evolutionary research since Pardi's work in the 1930s. Recent work on visual communication (Tibbetts 2002, 2004, Tibbetts & Dale 2004), social dominance (Liebig *et al*. 2005, Cant *et al*. 2006, Nonacs *et al*. 2006), caste (Sumner *et al*. 2006), and other topics (Giray *et al*. 2005) suggests paper wasps will continue to make interesting contributions to broad range of evolutionary questions.

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