Rearing conditions influence quality signals but not individual identity signals in *Polistes* wasps

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Given the diversity of animal signals, there has been recent interest in categorizing signals into probable functions according to their properties. For example, models predict that signals of quality should be costly and condition dependent, whereas signals of individual identity should be cheap and expressed independently of condition. Here, we test these predictions by comparing the condition dependence of signals of individual identity and quality in *Polistes* wasps. *Polistes fuscatus* wasps have black and yellow patterns on the face and abdomen that signal individual identity, whereas *Polistes dominulus* wasps have black and yellow facial patterns that signal aspects of quality related to dominance. We reared both species with and without supplemental food and examined the facial patterns of the resulting offspring. As predicted, food availability did not influence the development of identity signals in *P. fuscatus*. In strong contrast, *P. dominulus* wasps reared with supplemental food reared patterns that signaled higher levels of quality than *P. dominulus* reared without supplemental food. Interestingly, the identity and quality signals have different condition dependence, despite being composed of similar pigments, suggesting that signal function has a stronger influence on signal properties than pigmentation. Because body size is often correlated with quality signal elaboration, we also tested how food supplementation influenced offspring size. In both species, supplemented colonies produced smaller offspring than nonsupplemented colonies, suggesting that queens may invest in producing fewer, larger offspring in stressful environments. Key words: badge-of-status, condition dependence, individual recognition, paper wasps, *Passer domesticus*, signal properties. [Behav Ecol 18:602–607 (2007)]

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animals use variable colors, calls, and odors to communicate many kinds of information, including their quality, gender, species, kinship, and individual identity (Bradbury and Vehrencamp 1998; Dale 2006). With such diversity, it can be challenging to identify the meaning of a particular signal. Often, manipulative behavioral experiments can be used to identify the information conveyed by a signal. In other cases, it is not possible to realistically alter a signal within a natural behavioral context.

In the absence of detailed behavioral experiments, signal properties can sometimes be used to categorize signals into probable functions. Signals that convey different information are theoretically expected to have different properties (i.e., variance, modality, and developmental influences) (Dale 2006). The theoretically expected properties have been established for many signals, but experimental tests of some signal properties are lacking. Here, we will test whether signal elaboration is dependent on the signaler’s overall health and vigor (or condition). Models predict that individual identity signals will not be condition dependent (Dale et al. 2001), and lack of condition dependence is sometimes used as supportive evidence that a variable trait is likely to be an identity signal (Jarvi et al. 1987; Dale 2000). However, there have been no experimental tests of identity signal condition dependence.

Polistes wasps present a good opportunity to test how the meaning of a signal influences signal properties, as the genus contains 2 species with signals that appear remarkably similar. Both species have variable black and yellow facial patterns composed of similar pigments (Becker 1957; Ishay and Pertsis 2002). However, the signals have entirely different meanings; *Polistes fuscatus* has signals of individual identity, whereas *P. dominulus* has signals of agonistic quality (Tibbetts 2002; Tibbetts and Dale 2004). Here, we manipulate food availability during larval development to compare the condition dependence of these signals of individual identity and quality.

INDIVIDUAL IDENTITY SIGNALS

During individual recognition, an organism identifies an individual according to their distinctive characteristics (Dale et al. 2001). The characters used for individual recognition have no inherent meaning. Instead, the characters become meaningful after an organism learns to associate a specific combination of markings with a specific individual. Signals of individual identity are surprisingly common; they occur in diverse modalities (visual, chemical, acoustic) and species (from wasps to wolves). They are also used in a range of social contexts, including leks, cooperative groups, monogamous pairings, and dominance interactions (Whitfield 1987; Beecher 1989; Johnstone 1997; Dale et al. 2001; Dale 2006)  

Dale and colleagues modeled the properties of signals of identity, predicting that identity signals will not be condition dependent. Because identity signals evolve under frequency-dependent selection, rare phenotypes that impose relatively low costs will spread to high equilibrium frequencies. Phenotypes with high costs will not rise to an appreciable frequency in the population. As signals of identity are not expected to be costly, signal development is not expected to be condition dependent (Dale et al. 2001). Here, we manipulate food availability during *P. fuscatus* development for the first experimental test of identity signal condition dependence.

QUALITY SIGNALS

Quality signals convey information about the overall phenotypic and genetic constitution of their bearer (Andersson
1994). Unlike identity signals, quality signals convey independent meaning; within a signaling system, high-quality signals have consistent characteristics. Although most quality signal research has been performed on sexual signals used during mate choice, quality signals can also be used in other contexts such as social competition and predator deterrence (Brandt 2003; Kraaijeveld et al. 2004).

One thing all handicap quality signals have in common is that relative signal costs are expected to be condition dependent. For a given level of signal elaboration, individuals in good condition experience larger benefits per unit cost than individuals in poor condition (Grafen 1990; Maynard-Smith and Harper 2003; Searcy and Nowicki 2005; Getty 2006). Condition-dependent costs will maintain the honest association between signaled and true quality because the optimal degree of signal elaboration will vary with the signaler’s condition (Grafen 1990; Getty 2006). Indeed many studies have found a correlation between condition and sexual quality signal elaboration (Andersson 1994; Johnstone 1995). More compellingly, there are a number of carefully designed experiments that have shown that environment during signal development influences sexual signal elaboration; individuals with reduced food quality, quantity, or high parasite loads develop less elaborate signals than individuals developing in more favorable environments (review in Cotton et al. 2004). Although some questions remain, there is a general consensus that sexual signals of quality are typically condition dependent (Cotton et al. 2004; Tomkins et al. 2004).

In contrast to sexual signals, relatively little is known about the condition dependence of social signals that are used during competitive interactions with rivals (or badges-of-status). Badges are sometimes thought to be less strongly condition dependent than sexual signals because badges do not have costs associated with signal production. Instead, badges impose social costs associated with signal maintenance; low-condition individuals are expected to be less able to withstand the increased risk and/or aggression associated with maintaining a high-quality signal (Rohwer 1975; Maynard-Smith and Harper 1988; Senar 1999; Tibbetts and Dale 2004). In theory, the absence of costs at the moment of signal production could make badges less strongly condition dependent than sexual signals. However, if the optimal degree of signal elaboration varies with individual condition, individuals would be expected to assess their condition and signal at a level they can optimally maintain (Griffith et al. 2006).

Empirical studies on the condition dependence of social cost signals have produced mixed results. Most development research has been done in house sparrows, as the classic social cost signal is the black throat badge used during minor dominance contests in bird flocks (Senar 1999). Some studies indicate body condition and food quality during molt do not influence house sparrow badge development (Gonzalez et al. 1999; McGraw et al. 2003; Poston et al. 2005). However, 2 studies suggest that environment during early growth may influence badge elaboration (in house sparrows, Griffith et al. 1999; paper wasps, Tibbetts 2006). Here, we perform the first controlled manipulation of early developmental environment to test whether Polistes dominulus badge elaboration is influenced by environment during development.

Both P. fuscatus and P. dominulus paper wasps have variable black and yellow cuticular pigments that are used for social communication (Figure 1). Despite their similarities, the signals convey different information. Polistes fuscatus markings signal individual identity, whereas P. dominulus markings signal agonistic quality (Tibbetts 2002; Tibbetts and Dale 2004). Here, we compare signal condition dependence in P. dominulus and P. fuscatus. We reared colonies of both species under 2 nutritional conditions: 1) free foraging and 2) with supplemental food. We predict that larval diet will not influence the development of identity signals in P. fuscatus. In strong contrast, we predict that larval nutrition will influence quality signal development in P. dominulus. Polistes dominulus larvae reared with supplemental food are expected to develop color patterns associated with signaling higher levels of quality than larvae reared without supplemental protein.

**METHODS**

**Rearing offspring**

In late May 2002, nests of P. dominulus and P. fuscatus were collected from Chenango Valley, New York. Similarly sized nests containing eggs were chosen for the experiment. Foun-dresses were marked with Testor’s enamel paint, and each nest was mounted on the ceiling of a 14 × 15.5 × 20 cm wooden box with removable Plexiglas face (Nadeau and Stamp 2003). Prior to the experiment, wasps were provided with ad libitum water, honey–water (1:10 parts honey-water), and 2 third instar Manduca sexta caterpillars per day.

**Figure 1**

Top row: portraits Polistes dominulus, illustrating the variation in black coloration in the center of the clypeus. Bottom row: portraits of Polistes fuscatus, illustrating some of the variation in inner eye, brow, and clypeus patterns.
On 17 June, nests were divided into 2 treatments, with 8 nests per treatment. The supplemented treatment received ad libitum honey–water, water, and *Galleria mellonella* prey, and foraging was limited to a screen cage. The nonsupplemented treatment was allowed to forage freely on naturally occurring prey, but received no supplemental prey, though they received ad libitum honey–water. At the end of the study, there were 4 supplemented *P. fuscatus* colonies and 4 nonsupplemented *P. fuscatus* colonies. Six supplemented *P. dominulus* colonies and 3 nonsupplemented *P. dominulus* colonies were also rearer. Nests that failed before the end of the colony cycle and produced fewer than 5 offspring were excluded from the analyses.

### Facial pattern assessment

At the end of the experiment, wasps were dried and stored for facial pattern analysis. Later, each wasp’s face was photographed using a digital camera. Improper drying caused approximately 150 wasps to become too degraded for facial pattern analysis. The degraded wasps were evenly distributed between nests and treatments. Facial patterns of the degraded wasps could be partially assessed under a microscope. Although the patterns were not clear enough for detailed analysis, we could discern that wasps with every type of facial pattern were degraded. Consequently, their exclusion is unlikely to bias the results.

*Polistes fuscatus* have extremely variable color patterns. *Polistes fuscatus* facial patterns vary in the inner eye, eyebrow, clypeus edge, and middle clypeus. *Polistes fuscatus* abdominal stripes also vary, with each wasp having between 1 and 4 stripes. All patterns vary independently (Tibbetts 2002). *Polistes fuscatus* pay attention to the presence or absence of each type of facial pattern as well as the number of abdominal stripes. Consequently, we scored the presence or absence of each type of facial pattern and counted the number of abdominal stripes on each wasp. In sum, we assessed the facial patterns of 93 offspring from supplemented *P. fuscatus* colonies and 68 offspring from nonsupplemented *P. fuscatus* colonies.

We assessed signal phenotype in *P. dominulus* by analyzing a digital picture of each wasp face with Adobe Photoshop. Facial patterns were analyzed for “brokenness” as described in Tibbetts and Dale (2004). A wasp’s facial pattern brokenness is the best predictor of dominance and takes into account the number, size, and shape of black spots on the center of the clypeus. Briefly, 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 gives a single number, the “brokenness index.” One hundred and seventy-nine offspring from supplemented *P. dominulus* colonies were analyzed as well as 83 offspring from nonsupplemented *P. domninus* colonies.

In both species, head width at the widest point of the head was used to assess body size. All the wasp heads were photographed next to a ruler, and head width was analyzed using Adobe Photoshop. Head width is fixed at pupation, so it is considered a good measure of structural body size that reflects larval development (Gilboa and Nonacs 2006).

### Analysis

In *P. fuscatus*, we used a generalized linear model to estimate the effect of food supplementation on facial pattern. The model estimates the effect of treatment on nonnormal outcomes, like *P. fuscatus* color patterns. We used generalized estimating equations (GEEs) to account for within-nest correlation. The analysis was done using GEE and PROC GENMOD in SAS (version 9.1, SAS Institute 2004). We analyzed 5 pattern parameters that vary independently: inner eye stripe, eyebrow stripe, clypeus edge stripe, black middle clypeus spot, and number of yellow abdominal stripes. A separate analysis was performed for each parameter. Each analysis compared the probability of offspring having the specified pattern in supplemented versus nonsupplemented nests after controlling for greater pattern similar among offspring from the same nest.

In *P. dominulus*, we compared offspring facial pattern brokenness and head width in supplemented versus nonsupplemented nests by fitting a mixed linear model with fixed treatment effects. We allowed the error variance to vary by treatment group and included nest as a random factor. The analysis was performed using the PROC MIXED procedure of SAS statistical software (version 9.1, SAS Institute 2004).

In both species, we analyzed how head width varied in supplemented and nonsupplemented colonies using a mixed model analysis of variance (ANOVA) with nest as the random factor.

### RESULTS

**Polistes fuscatus**

As predicted, *P. fuscatus* reared on supplemented and nonsupplemented diets had similar color patterns (Table 1). Each supplemented versus nonsupplemented *P* value gives the

### Table 1

**Effects of protein supplementation on the color patterns of offspring from *Polistes fuscatus* nests**

<table>
<thead>
<tr>
<th>Wasp pattern</th>
<th>Parameter</th>
<th>Estimate</th>
<th>Standard error</th>
<th>Z</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inner eye</td>
<td>Intercept</td>
<td>0.14</td>
<td>0.20</td>
<td>0.7</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>Supplemented versus nonsupplemented</td>
<td>0.40</td>
<td>0.36</td>
<td>1.1</td>
<td>0.28</td>
</tr>
<tr>
<td>Brow</td>
<td>Intercept</td>
<td>0.44</td>
<td>0.20</td>
<td>2.25</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td>Supplemented versus nonsupplemented</td>
<td>0.18</td>
<td>0.37</td>
<td>0.48</td>
<td>0.63</td>
</tr>
<tr>
<td>Black midclypeus</td>
<td>Intercept</td>
<td>−1.65</td>
<td>0.33</td>
<td>−4.96</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td></td>
<td>Supplemented versus nonsupplemented</td>
<td>−0.13</td>
<td>1.05</td>
<td>1.9</td>
<td>0.90</td>
</tr>
<tr>
<td>No. of stripes</td>
<td>Intercept</td>
<td>−0.21</td>
<td>0.16</td>
<td>−1.27</td>
<td>0.21</td>
</tr>
<tr>
<td></td>
<td>Supplemented versus nonsupplemented</td>
<td>0.14</td>
<td>0.85</td>
<td>0.17</td>
<td>0.86</td>
</tr>
<tr>
<td>Clypeus edge</td>
<td>Intercept</td>
<td>1.9</td>
<td>1.3</td>
<td>1.44</td>
<td>0.14</td>
</tr>
</tbody>
</table>

Results of 5 different analyses are shown. Each bold *P* value gives the probability that individuals from supplemented colonies differ from nonsupplemented colonies in the specified color pattern. None are statistically significant, indicating that protein supplementation did not influence color pattern development. Generalized linear models were used for statistical analysis and GEEs accounted for within-nest correlation.
probability that facial patterns were distributed nonrandomly across treatments. In every case, the probabilities are greater than 0.05, indicating that food supplementation did not influence \textit{P. fuscatus} facial pattern development. Significant intercept \(P\) values indicate certain patterns were very rare. For example, many \textit{P. fuscatus} had yellow eyebrow stripes, so the intercept \(P\) value shows the distribution of “brow” was significantly different from a random distribution of half with yellow brows and half without yellow brows.

Supplemented nests produced smaller offspring than nonsupplemented nests. Using a mixed model ANOVA with nest as a random factor, the head widths of offspring from supplemented colonies were smaller than head widths of offspring from nonsupplemented colonies (whole model \(r^2 = 0.23, F_{1.8} = 4.45, P = 0.04\)). Mean head width of offspring from supplemented colonies was 3.8 mm, whereas mean head width of offspring from nonsupplemented colonies was 4.0 mm.

\textbf{Polistes dominulus}

\textit{Polistes dominulus} reared on a supplemented diet had significantly more broken clypeus patterns than those reared on nonsupplemented diets. (Table 2, Figure 2). The significant intercept \(P\) value indicates that facial patterns were more similar within than between nests (\(P = 0.0004\)). However, offspring from the same nest were reared in similar environments and share similar genotypes, so it is difficult to assess whether genotype or environment accounts for the within-nest similarity.

Previous work indicates that larger wasps have more broken facial patterns (Tibbetts and Dale 2004; Tibbetts 2006), but the relationship between food supplementation and facial pattern brokenness was not merely a consequence of supplemented colonies producing larger offspring. In fact, supplemented \textit{P. dominulus} colonies produced offspring with smaller head widths than nonsupplemented colonies (Table 2, \(P = 0.04\)). Mean head width in supplemented colonies was 3.53 mm. Mean head width in nonsupplemented colonies was 3.63 mm. The smaller size of supplemented offspring caused a negative relationship between head width and facial pattern brokenness across the entire sample (\(r^2 = 0.23, F_{1.9} = 3.1, P = 0.05\)). Within each treatment, there was no relationship between facial pattern brokenness and head width (supplemented \(r^2 = 0.11, F_{1.6} = 1.46, P = 0.29\); nonsupplemented \(r^2 = 0.13, F_{1.3} = 2.8, P = 0.1\)).

\section*{Discussion}

\textbf{Food supplementation and signaling}

\textit{Polistes dominulus} and \textit{P. fuscatus} paper wasps were reared under 2 treatment conditions: 1) with supplemental food and 2) without supplemental food. \textit{Polistes fuscatus} identity signals showed no evidence of condition dependence; food supplementation did not influence color pattern development. In contrast, \textit{P. dominulus} quality signals were strongly condition dependent. Larvae reared with supplemental food developed facial patterns that signaled a higher level of quality than larvae reared without supplemental food.

These results provide the first experimental support for the prediction that identity signals development is not condition dependent. Free-foraging \textit{Polistes} are food limited (Rossi and Hunt 1988; Hunt and Dove 2002), so we increased larval food availability by providing unlimited supplemental food to certain nests. Small differences in nutrition during early development produces lasting effects on adult condition because early developmental perturbations have the strongest phenotypic effects (Lindstrom 1999; Metcalfe and Monaghan 2001). Nevertheless, there were no significant differences in the facial patterns of offspring reared on supplemented and nonsupplemented diets. Nests under both treatments produce offspring with a diverse range of variable facial patterns. These results support previous observational work that suggested that \textit{P. fuscatus} identity signals are not condition dependent. Tibbetts (2002) found that \textit{P. fuscatus} color patterns are not correlated with body size or dominance rank. Therefore, experimental and observational tests have found no evidence that \textit{P. fuscatus} identity signals are condition dependent, supporting the model prediction that lack of condition dependence may be a diagnostic character of identity signals (Dale et al. 2001).

In contrast to \textit{P. fuscatus}, \textit{P. dominulus} signal development was strongly influenced by supplemental feeding. \textit{Polistes dominulus} reared with supplemental food developed facial patterns associated with higher levels of agonistic quality than \textit{P. dominulus} reared without supplemental food. The relationship between badge phenotype and early nutrition is logical. Adult condition is influenced by developmental environment (reviews in Lindstrom 1999; Metcalfe and Monaghan 2001; Qvarnstrom and Price 2001), and badges-of-status convey information about adult condition. The condition dependence of \textit{P. dominulus} badges seems at odds with other studies indicating environmental stress does not influence badge development. However, the studies that found no relationship between badge elaboration and the environment imposed environmental stressors in a brief window around badge development (Gonzalez et al. 1999; McGraw et al. 2003; Poston et al. 2005). In contrast, variation

\begin{table}[htb]
\centering
\caption{Effects of protein supplementation on the facial pattern brokenness and head width of offspring from \textit{Polistes dominulus} nests}
\begin{tabular}{lllrrr}
\hline
Effect & Estimate & Standard error & \(T\) & \(P\) \\
\hline
Intercept & 2.6 & 0.45 & 5.75 & 0.0004 \\
Supplemented versus nonsupplemented & 1.6 & 0.57 & 2.71 & 0.007 \\
Head width & -1530 & 752 & -2.0 & 0.04 \\
\hline
\end{tabular}
\end{table}

Mixed linear model with fixed treatment effects was used for statistical analysis, allowing the error variance to vary by treatment group and including nest as a random factor. Supplementation significantly influenced facial pattern development and head width.

\section*{Figure 2}

Mean (+standard deviation) brokenness of \textit{Polistes dominulus} facial patterns. Offspring from colonies with supplemental food had facial patterns that signaled a higher level of quality than offspring from colonies without supplemental food (\(P = 0.007\)).
in early developmental environment has a consistent influence on badge elaboration. Griffith (1999) used a brood swap experiment to show that the environmental factors influence badge development; house sparrows reared by higher quality social fathers had bigger adult badges than house sparrows reared by lower quality social fathers. In addition, in natural P. dominulus nests, late eclosing wasps develop more elaborate badges than early eclosing wasps, perhaps because environmental conditions become more benign as the colony cycle progresses (Tibbetts 2006). Therefore, physical environment can influence badge elaboration, and the dichotomy between agonistic and sexual signal development may not be as simple as previously thought. More manipulative experiments are clearly needed to pinpoint how the timing and severity of environmental stress influence quality signal development. Generally, we expect that environmental perturbations with lasting effects on adult condition will influence the elaboration of any reliable signal of quality.

**Pigment and signaling**

There has been recent interest in classifying visual signals according to their pigments. Pigments differ biochemically and have different physiological roles in the body. For example, in vertebrates, carotenoid pigments must be acquired from the diet, whereas melanin pigments can be synthesized (Olson and Owens 1998). Consequently, carotenoid-based signals are often assumed to be condition dependent, whereas melanin-based signals are typically considered noncondition dependent.

Although pigment research has been fruitful, our results with Polistes indicate that pigments are less important than signal function in determining signal properties. Individual identity and quality signals in Polistes wasps are composed of yellow (pterine) and black (eumelanin) pigments in the cuticle (Becker 1937; Ishay and Pertsis 2002). Nevertheless, the signals have different meanings and respond differently to the developmental environment. Therefore, signal function seems to drive condition dependence, whereas pigment composition is not a consistent method of categorizing signals.

**Size and developmental environment**

In both species, food-supplemented colonies produced offspring with smaller heads than nonsupplemented colonies. Head width is fixed during pupation and reflects larval resource allocation (Gilboa and Nonacs 2006), so these results suggest that maternal resource allocation varied between the 2 environments.

The smaller body size of offspring from supplemented colonies initially appears counterintuitive. Supplemented colonies had more food, yet produced smaller offspring. However, the result makes more sense after considering how the benefits of producing large offspring vary by environment. In harsh environments, it may be advantageous to produce fewer, larger offspring who can withstand environmental stress (Bernardo 1996). For example, in wild P. dominulus nests, large workers survive longer than smaller workers (Tibbetts EA, unpublished data), suggesting that larger offspring may be favored under harsh foraging conditions. A number of studies in other species have found a similar response to environmental stress; mothers in harsh environments concentrate available resources to produce fewer, larger offspring (Qian and Chia 1991; Glazier 1992; Reznick and Yang 1993).

**Information content of signals**

This development experiment corroborates behavioral work indicating that P. dominulus and P. fuscatus visual signals convey different information (Tibbetts 2002; Tibbetts and Dale 2004). The lack of condition dependence in P. fuscatus identity signals indicates that identity signals convey no specific, independent information. Instead, the variable characters become meaningful when they are learned in context (Dale 2006). In contrast, the condition dependence of P. dominulus quality signals indicates that the quality signals convey independent information about signaler quality.

Developmental manipulation provides a useful method of assessing the specific information conveyed by a quality signal (Hunt, Bussiere, et al. 2004). Environmental perturbations are thought to alter the way an individual allocates resources to different components of quality (Zera and Harshman 2001; Hunt, Brooks, et al. 2004), so developmental experiments may be used to determine which aspects of quality remain linked to the signal across a range of environments. For example, P. dominulus facial patterns are typically correlated with body size; larger wasps have more broken (higher dominance) facial patterns (Tibbetts and Dale 2004; Tibbetts 2006). Supplemental feeding had opposite effects on body size and brokenness, thereby eliminating the relationship between body size and brokenness in this experiment. Offspring from supplemented colonies were smaller, but they still advertised a higher level of quality than offspring from nonsupplemented colonies. Therefore, facial pattern brokenness is unlikely to be a signal of body size, instead, it may convey information about aspects of the bearer’s quality linked to early nutrition and relative dominance. Further experiments will be useful to provide a more detailed analysis of the specific information conveyed by quality signals. In particular, it will be interesting to compare the information conveyed by quality signals used in a range of contexts; does the context in which a signal is used influence the information it conveys?

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