



Heightened Condition Dependence of a Sexually Selected Signal in Male *Polistes dominulus* Paper Wasps

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Abstract

Sexually selected signals are theoretically expected to exhibit heightened condition dependence compared to non-signaling traits. This link to condition enables sexual signals to provide information regarding individual quality and also provides a mechanism that allows animals to develop signals that accurately reflect their abilities. Most previous work on sexual signal condition dependence has focused on signals that have clear developmental costs, while less is known about the development of other types of quality signals. Male *Polistes dominulus* paper wasps have yellow-on-black abdominal spots that are important signals during female choice and male–male competition. These signals lack obvious production costs, as males are covered in yellow and black patterns composed of the same pigments. Here, we assess signal condition dependence by testing whether larval diet has a stronger influence on the development of male spots than on the development of control traits composed of the same pigments. Males reared on *ad libitum* diets developed elliptical spots similar to those seen on dominant, attractive males, while males reared on restricted diets developed irregularly shaped spots similar to those seen on subordinate, unattractive males. Remarkably, the development of a control trait composed of the same yellow and black pigments was not influenced by larval diet. Therefore, sexually selected signals can be developmentally decoupled from traits comprised of the same pigments. Condition dependence of sexually selected signals is likely to be a widespread solution to the challenge of developing sexually selected signals that accurately convey information about individual quality.

Introduction

Males of many species have sexually selected ornaments that are used during aggressive competition and non-aggressive mate choice. These signals provide benefits; individuals with more elaborate ornaments are more successful during competition and are more preferred by females than males with less elaborate ornaments (Andersson 1982; Johnstone 1995). At the same time, the benefits of ornamentation are thought to be counterbalanced by the substantial costs associated with producing and/or maintaining elaborate ornaments (Zahavi 1975; Grafen 1990).

Much research on sexually selected ornaments has focused on the factors that prevent low-quality individuals from signaling that they are of high quality.

A key mechanism thought to maintain ornament accuracy over an animal's lifetime is condition dependence (Rowe & Houle 1996). 'Condition' is defined as the pool of resources allocated to traits that enhance fitness (Rowe & Houle 1996; Hill 2011). Condition is influenced by the environment (e.g., resource availability) and genotype (e.g., some genotypes are more successful in acquiring resources; Hunt et al. 2004; Tomkins et al. 2004). As condition is influenced by both environmental and genetic factors, linking ornament elaboration to an animal's condition is a good way for a signal to capture broad information about its bearer's overall phenotypic and genetic constitution. Handicap models predict that sexual ornaments will be more condition dependent than non-ornamental traits (Cotton et al. 2004).

Although condition dependence is often thought to be a general feature of sexually selected ornaments, experimental evidence for ornament condition dependence is surprisingly limited. Much evidence for sexual signal condition dependence is based on correlations between ornament elaboration and measures of condition (Andersson 1982). There are also some experimental tests of trait condition dependence that examine whether food availability influences ornament development. The best of these studies compares condition dependence of ornamental and control traits, showing that sexual traits are more condition dependent than non-ornamental traits (Cotton et al. 2004; Bonduriansky & Rowe 2005). More recently, Johnstone et al. (2009) challenged the theoretical basis of ornament condition dependence with a model suggesting that selection may produce sexually selected ornaments that are less condition dependent than non-ornamental traits.

The condition dependence of pigment-based ornaments has been a particularly dynamic research area (Hill & Montgomerie 1994; McGraw et al. 2002; Griffith et al. 2006). Much of this work has focused on how pigment type influences condition dependence. Some argue that the phenotype of a trait has deterministic effects on the development and function of that trait. As a result, traits composed of certain pigment types are more likely to be condition dependent and function as sexual signals than signals composed of other pigment types. For example, carotenoids are physiologically essential and must be acquired from the diet, while melanins can be synthesized *de novo*. As a result, carotenoid traits are sometimes assumed to be condition dependent, while melanin traits are sometimes assumed to lack condition dependence (reviewed in Griffith et al. 2006; McGraw & Hill 2006). Others argue that all sexual ornaments will be condition dependent, regardless of whether the pigments that comprise the ornament are inherently costly or limited. Given these questions about the relationships between animal coloration, sexual signaling and condition dependence, there is a surprising lack of research comparing the condition dependence of known sexual signals with control traits composed of similar pigments.

Here, we test the hypothesis that sexually selected signals show heightened condition dependence compared to control traits composed of the same pigments. We focus on the yellow-on-black spots of male *Polistes dominulus* paper wasps that function as sexually selected signals (Izzo & Tibbetts 2012). Males with more elliptical yellow spots are more likely to win fights with other males and are also more likely to be chosen as mates than males with irregular spots. Male spot variation was quantified using a spot shape index (SI, Fig. 1, details of SI calculation in Methods). Males with lower SI are preferred over males with higher SI.

Testing the condition dependence of male spots is particularly interesting because wasps' entire bodies are covered in yellow and black stripes and spots. As a result, we can compare the condition dependence of sexual signaling traits with other traits composed of the same pigment that are not involved in sexual selection. Paper wasp coloration is composed of melanins and pterins. These pigments are not thought to have substantial production costs, although the costliness of pigments may vary somewhat across systems (Stoehr 2006). For example, pterins are nitrogen rich, and nitrogen is likely to be more limited in herbivores than carnivores. As a result, pterin-based signals may have higher relative production costs in herbivores, like cabbage white butterflies (Morehouse & Rutowski 2010), than carnivores, like paper wasps.

We tested whether natal nutrition influences the sexually selected signal in male *P. dominulus* more than control traits. Few experimental tests of the condition dependence of sexual signals include control traits; fewer still have control traits that could be expected to share the same developmental pathway (Cotton et al. 2004). Natal nutrition influences adult paper wasp condition (Tibbetts & Curtis 2007; Tibbetts 2010), so altering larval nutrition is a good way to test trait condition dependence. We subjected wasp nests to diet treatments where the number of caterpillars available as a food source for developing wasp larvae was controlled. Half of the nests experienced restricted caterpillar availability, while the others received unlimited caterpillars. If the male spots are condition dependent, we expect that males from nests with restricted caterpillars will develop spots that

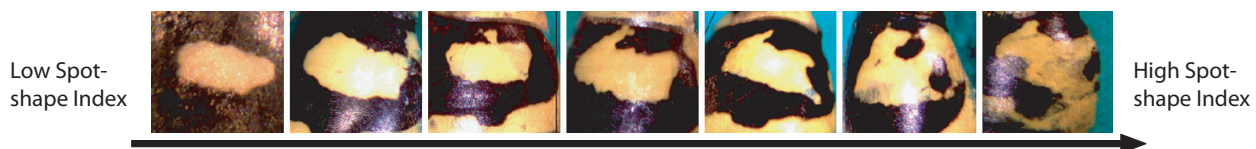


Fig. 1: Array of male dorsal abdominal spots, arranged from low-to-high spot shape index (SI). Males with low SI (left) are more dominant and more preferred as mates than males with high SI (right).

signal lower quality than males from nests with unlimited caterpillars. The control patterns are not predicted to differ between treatment groups.

Methods

Male *P. dominulus* wasps experience strong sexual selection. Paper wasps have a lekking mating system where males congregate at landmarks and compete over small mating territories. Females visit leks to choose mates and appear to assess multiple males during repeated visits before selecting a mate (Beani 1996). Male wasps are produced at the end of the colony cycle and only live a few months. Females mate, overwinter, and found nests the following year.

In early spring, 20 *P. dominulus* foundresses and their nests were collected from sites around Ann Arbor, MI, and brought to the laboratory. Each foundress and her nest were placed into a nest box and randomly assigned to one of the two diet treatments. One group received sufficient *Galleria mellonella* caterpillars that they did not consume all the caterpillars, while the other group received approximately half as many caterpillars per nest cell. Nests in the low-caterpillar diet treatment (hereafter low) ate all the caterpillars they received, while nests in the high-diet treatment (hereafter high) usually left a small amount of food uneaten. Caterpillars are consumed by both adults and larvae and provide the protein and fat source for each. Adults can survive on sugar alone for long time periods, but developing larvae require caterpillars for growth.

The number of caterpillars eaten by each colony was recorded three times per week to ensure that high- and low-caterpillar treatments were eating significantly different amounts. High-caterpillar colonies ate more caterpillars per nest cell per day than low-caterpillar colonies; high: $\bar{x} = 0.034$, standard deviation = 0.0018 caterpillars per nest cell per day and low: $\bar{x} = 0.0156$, standard deviation = 0.00021 caterpillars per nest cell per day. All nests were provided with unlimited water, sugar and paper for nest construction. Nests were monitored throughout the spring and summer. Nests that failed prior to the end of the season or produced only females were excluded from the study. As males emerged, they were removed from nests and were weighed on a scale accurate to 0.001 g and photographed for the analysis of their color patterns. Then, head width at the widest part of the head was assessed as the measure of structural size.

In total, 76 males from 14 nests (six high caterpillar, eight low caterpillar) were collected and measured for

the experiment. Each male was weighed while alive and then frozen prior to photographic analysis. Photographs were taken of male dorsal abdominal spots (i.e., the sexually selected signal in this species, Izzo & Tibbetts 2012; Figs 1 and 2), as well as thoracic stripes that were used as the control trait (Fig. 2). Previous work in this system has shown that abdominal spots have high levels of intraspecific variation, are sexually dimorphic, and function as signals during male–male competition and female choice (Izzo & Tibbetts 2012). During courtship and competition, males appear to display the spots to conspecifics (Izzo 2011). In contrast, thoracic stripes are not sexually dimorphic and the size and position of thoracic stripes make these stripes difficult for wasps to see during social interactions (Izzo 2011). Control traits sensu (Cotton et al. 2004) are traits ‘similar in kind to ornamental traits’ but non-sexual. Control traits are used to test whether the sexually selected signal is more condition dependent than other traits. The alternative is that all color patterns are influenced by diet similarly such that males reared on high-quality diet have different overall color patterning than males reared on poor diet.

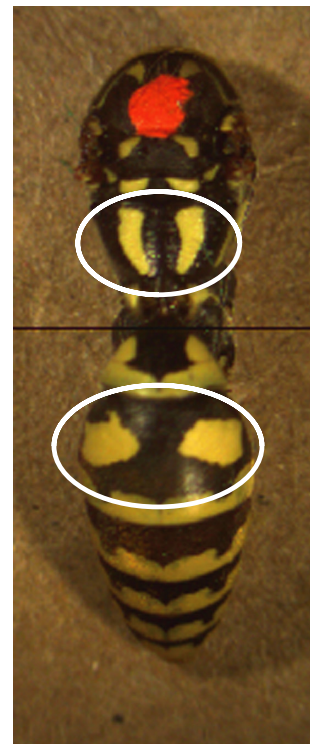


Fig. 2: Dorsal view of male wasp, showing the location of control traits (thoracic stripes, top circle) and male ornaments (dorsal abdominal spots, bottom circle). The red thorax mark is paint applied during experimentation.

Male *P. dominulus* paper wasps with more elliptically shaped spots are more likely to win fights with other males and are also more likely to be chosen as mates over males with irregularly shaped spots (Izzo & Tibbetts 2012). To capture and describe spot shape variation, a 'spot shape index' was created. This index compares the average size of the spot to an idealized ellipse calculated by the length and height of the spots. Males with elliptical spots have low SI values, while males with irregularly shaped spots have high SI values. For each male in the experiment, the length (L), height (H) and area (A) of the dorsal abdominal spots were measured in pixels. The SI was calculated using the formula $SI = A/(\pi * 1/2L * 1/2H)$ (Izzo & Tibbetts 2012). For the control trait, dorsal thoracic stripes, the yellow stripe area (in pixels) was measured. Thoracic stripe area was not size-corrected, although larger wasps have a larger thorax and therefore larger thoracic stripes. Some statistical models include size as a factor to ensure that any thoracic stripe differences between high- and low-diet treatments were not due to body size. All photographs were taken using Infinity Analyze software with a camera mounted on a microscope. Photoshop CS was used for all photographic measurements.

A challenge of comparative studies is establishing the appropriate control traits (Cotton et al. 2004). This study compares similar signaling and control traits, providing a relatively powerful test of how trait function influences condition dependence. A potential weakness of this study is that we measured different aspects of the signaling and control traits (shape of the signaling trait, area of the control trait). These parameters were measured because they are most biologically meaningful; signal receivers pay attention to the shape of the signaling trait rather than its size (Izzo & Tibbetts 2012). However, it is possible that shape and size of color patches are somewhat developmentally distinct. As a result, future studies that compare condition dependence of size-based signaling traits and size-based control traits composed of the same pigments will be useful.

To determine how coloration and body size were influenced by natal diet, mixed linear models with restricted maximum likelihood (REML) estimation were run with diet and nest (as a random factor) included as predictors. Nest was included as a random factor to account for any within-nest similarity. Four separate models were run to determine how diet and nest were associated with body weight, body size, the signaling trait (male SI), and the control trait (thoracic stripes).

We ran additional models to test the combined effect of body size, diet, and nest on both SI and thoracic stripe area. These additional models are particularly important for thoracic stripe area, as area is a body size-dependent variable. Larger wasps have larger thorax, so they will also have larger thoracic stripes. These models were mixed linear model with REML estimation, including diet, head width, and nest (random factor) as the predictors. To ensure that collinearity between color traits and body size did not interfere with the reliability of these models, we tested the relationships between size and both color patterns. Head width was correlated with both thoracic stripes ($r^2 = 0.15$, $F_{1,74} = 12.3$, $p = 0.001$) and SI ($r^2 = 0.11$, $F_{1,74} = 10.4$, $p = 0.002$). However, the relationships did not reduce model accuracy. In particular, variance inflation factors were <1.2 and 10 is the traditional cut-off. Therefore, model fit is not reduced by collinearity (Zar 1998). For each model, we present estimated marginal means (EMM) \pm SE for individuals from the high and low diet. Cohen's d was also calculated as a measure of the magnitude of the difference between color traits in high- and low-diet treatments. Analyses were run using SPSS v. 21.

Results

Diet treatment had a significant impact on male size and weight. Males reared on high-caterpillar diets were larger and weighed more than males reared on low-caterpillar diets (weight: $p < 0.0001$, $F_{1,10.7} = 69.1$, high = 0.101 ± 0.0026 g, low = 0.072 ± 0.0024 g; head width: $p = 0.002$, $F_{1,8.0} = 18.7$, high = 3.46 ± 0.04 mm, low = 3.2 ± 0.037 mm).

The sexually selected male dorsal abdominal spots are condition dependent (Fig. 3). Males reared on a high-caterpillar diet signal higher advertised quality (smaller SI) than males reared on a low-caterpillar diet ($p = 0.02$, $F_{1,11.2} = 7.1$, EMM high = 1.39 ± 0.096 , low = 1.7 ± 0.085 , Cohen's $d = 0.61$). SI is a size-independent measure; yet to demonstrate that the increase in male size on the high-caterpillar diet was not responsible for the condition dependence of SI, we ran a model to test whether SI was predicted by both diet and size (with nest as a random factor). In the model, diet treatment, but not body size, is associated with variation in male signals (diet, $F_{1,15} = 4.4$, $p = 0.05$, EMM high = 1.4 ± 0.1 , low = 1.7 ± 0.09 ; head width $F_{1,72} = 0.31$, Cohen's d calculated using parameter estimates when head width 3.3 mm = 0.49). Therefore, the condition dependence of the male spots is not due to the increase in male size in the high-caterpillar treatment (Fig. 3).

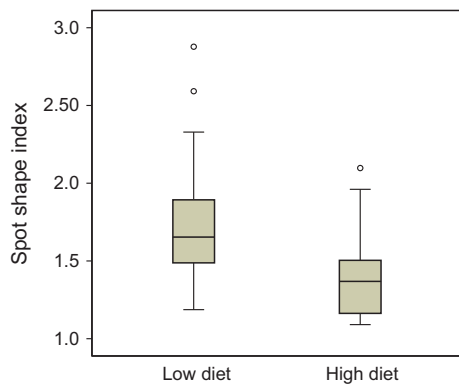


Fig. 3: Male spot shape is condition dependent, with males reared on high-caterpillar diets having significantly smaller spot shape index (SI) than males reared on low-caterpillar diets. Males with low SI spots are more dominant and more preferred as mates than males with high SI. Box indicates the 25th, 50th, and 75th percentile; the whiskers reflect the minimum and maximum except for the dots, which reflect extreme data points that are more than three interquartile ranges from other data points.

The control trait, male thoracic stripes, is not condition dependent. There is no difference in thoracic stripe area of males reared on different diets (diet $F_{1,11} = 1.4$, $p = 0.26$; EMM high = 4519 ± 432 pixels; low 3835 ± 379 pixels; Cohen's $d = 0.28$). There is also no difference in the area of stripes for males reared on a high-caterpillar diet vs. males reared on a low-caterpillar diet when body size is included in the model (diet $F_{1,12,9} = 1.05$, $p = 0.33$, EMM high = 4486 ± 431 pixels, low $\bar{x} = 3877 \pm 383$ pixels; head width $F_{1,66} = 0.22$, $p = 0.6$; Cohen's d calculated using parameter estimates when head width $3.3 \text{ mm} = 0.24$; Fig. 4).

Discussion

The strong influence of larval diet on adult signal expression illustrates that the dorsal abdominal spots of male paper wasps are condition dependent. Males reared on a high-caterpillar diet developed spots with smaller SI than males reared on a low-caterpillar diet. Previous work has shown that males with small SI are more dominant and more preferred as mates than males with larger SI (Izzo & Tibbetts 2012). Therefore, larval diet influences elaboration of the sexually selected ornament in male paper wasps. Remarkably, development of the control traits composed of the same pigments was not significantly influenced by larval diet. Further, effect size calculations illustrate that diet had a larger effect on the sexual signaling trait than on the control trait. Therefore, general male

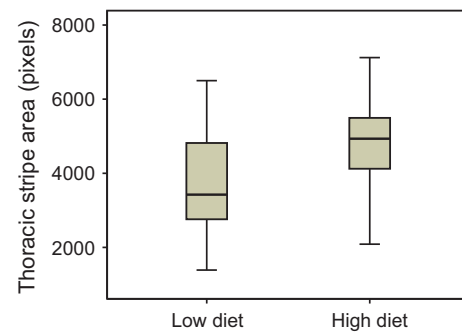


Fig. 4: The control trait, thoracic stripes, is not condition dependent. There is no difference in area of the stripe between high- and low-caterpillar diets. Box indicates the 25th, 50th, and 75th percentile, while the whiskers reflect the minimum and maximum.

coloration is not condition dependent. Instead, ornament condition dependence is a highly specific adaptation that facilitates the development of accurate signals.

Theory suggests that condition-dependent ornaments likely provide valuable information for females assessing potential mates. Genic capture models propose that condition-dependent ornaments provide information about the genetic quality of their bearer because a large number of loci in the genome contribute to variation in condition (Rowe & Houle 1996; Kokko & Heubel 2008 but see Hingham 2013). Condition-dependent ornaments also provide direct information about their bearer's nutritional state and ability to acquire resources. In some taxa, males may directly contribute these resources to females or offspring (Andersson 1982; Johnstone 1995). In other taxa, male nutrition influences physiological functions, including ejaculate quality (Boggs 1990; Gwynne & Brown 1994). A recent meta-analysis found broad, if weak, evidence that the elaboration of male ornaments is positively associated with sperm viability (Mautz et al. 2013). In paper wasps, females must store sperm for up to 11 mo, and there are no opportunities for re-mating in the spring, as males do not overwinter (Jandt et al. in press). Therefore, female fitness is strongly influenced by male sperm quality, which may be dependent on male natal nutrition (Izzo 2011).

An interesting aspect of this study is that we compared the condition dependence of two traits composed of the same pigments. Traits composed of the same pigments are sometimes thought to share similar developmental trajectories (McGraw et al. 2002; Griffith et al. 2006; McGraw & Hill 2006). However, the results of this study indicate that the condition

dependence of a trait is not correlated with the mechanisms that produce the trait, but rather with the signaling context in which it is used. Sexually selected ornaments that signal quality are condition dependent, while traits that do not convey information about quality are not. In the future, detailed biochemical analyses of paper wasp color patterns will be useful, as color traits can be composed of complex mixtures of multiple different pigments (Grether et al. 2001). This study adds to a growing body of evidence indicating that it is overly simplistic to categorize traits according to pigment composition (Griffith et al. 1999; Siefferman & Hill 2003; Siitari et al. 2007; Tibbetts & Curtis 2007). Ornaments composed of a broad range of pigment types can signal condition and quality (Szamado 2011).

A critical, but rarely examined aspect of research on condition dependence is the evolution of condition dependence. Is heightened condition dependence a cause or consequence of sexual signaling? Internal factors like a trait's developmental processes may predispose certain traits to be condition dependent, and these traits may most commonly become sexually selected signals. Alternatively, a predisposition to condition dependence may not be required. Instead, condition dependence may be evolvable, with no required developmental tendency toward condition dependence (Endler 1992; Badyaev 2004; Cotton et al. 2004). Although this study does not directly test how condition dependence evolves, we found that two traits with the same apparent physiological basis have differential developmental trajectories. As a result, condition dependence appears to be flexible and evolvable rather than constrained by factors such as pigmentation. There is also evidence that condition dependence of body structures is evolvable; sexually selected rhinoceros beetle horns are more condition dependent and more responsive to insulin-like signaling during development than other body structures (Emlen et al. 2012). Heightened sensitivity to the insulin-like signaling pathway may be a common mechanism linking sexually selected traits to condition (Warren et al. 2013). Exploring the evolutionary patterns of trait condition dependence presents experimental challenges, but is essential to understand how and why variation in condition dependence occurs.

The results of this study also show that male body size and weight are influenced by natal nutrition. Better fed larvae become larger adults than poorly fed larvae. This is consistent with extensive research across diverse taxa showing that body size is influenced by nutrition (Smith & Lyons 2013). In paper wasps, females choose mates based on male abdominal spots

but do not appear to choose males based on body size (Izzo & Tibbetts 2012). Perhaps, abdominal spots are easier for females to assess than body size or abdominal spots provide more useful information about male quality than size. The lack of relationship between male body size and mating success is consistent with another study on mate choice in *Ropalidia* wasps (Shilpa et al. 2010).

In summary, male paper wasps have abdominal spots that are a condition-dependent ornament used during competition and mate choice. Males also have thoracic stripes composed of the same pigments, but the stripes are not condition dependent. These results add to a growing body of work suggesting that condition dependence is evolvable rather than being constrained by factors such as pigment type. As a result, sexually selected signals may be developmentally independent from non-signaling traits comprised of the same pigments. Much work on the function and development of animal ornaments has focused on a small subset of well-studied groups, especially birds. New groups such as paper wasps may provide novel insight into the development and evolution of ornaments.

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