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The Role of Climatic Factors in the Expression of an Intrasexual Signal in the Paper Wasp *Polistes dominulus*

Jonathan P. Green, Charles Rose & Jeremy Field

School of Life Sciences, University of Sussex, Brighton, UK

Correspondence
Jonathan P. Green, Mammalian Behaviour and Evolution Group, University of Liverpool, Leahurst Campus, Neston, CH64 7TE, UK.
E-mail: jpgreen@liv.ac.uk

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Abstract

Within a species, variation in the use of sexual signals is observed between different populations. For intersexual traits, differences in the environmental conditions experienced by populations can play an important role in driving variation in male ornaments and female preferences. However, little is known about the factors maintaining variation in intrasexual traits used in competition. In this study, we investigate the role of climatic conditions in maintaining variation in the expression of an intrasexual signal in the paper wasp *Polistes dominulus*. The results of an experiment in which pupae were housed under different temperature and humidity conditions revealed a strong effect of temperature during pupal development on the expression of the signal. Furthermore, a comparison of survival and body weight between wasps reared at different temperatures indicates that signal expression exhibits phenotypic plasticity in response to developmental temperature. The effect of temperature on signal expression is consistent with patterns of signal expression observed across populations in the wild and suggests that climatic conditions may act to constrain signal expression in some populations but not in others, driving variation in signal use within *P. dominulus*. Environmental conditions may therefore be important in defining the scope for intrasexual signalling in animal populations and, in doing so, may play a role in maintaining variation in intrasexual traits in the face of sexual selection.

Introduction

Within a species, the signal value of a trait under sexual selection is not always constant but can vary between populations (Wilczynski & Ryan 1999). In the case of intersexual signals (i.e. those that function in mate choice), intraspecific variation is observed in the design and elaboration of male ornaments (Hill 1994; Endler & Houde 1995; Safran & McGraw 2004), as well as in the strength and direction of female preferences for those ornaments (Griffith et al. 1999b; Dunn et al. 2008; Takahashi et al. 2008). Less is known about inter-population variation in intrasexual signals, which signal quality to same-sex rivals during competition for resources, although several studies have shown that these signals also vary in form and function between populations in some species (Baird et al. 1997; Garamszegi et al. 2006; Green & Field 2011). Given that sexual selection is expected to erode variation in traits that affect reproductive success within species (Bussière et al. 2008), the existence of inter-population variation in such traits is puzzling. Identifying the factors that drive variation in sexually selected traits is therefore a useful step towards understanding how additive genetic variation in both signals and receiver responses can be maintained in the face of sexual selection (Hill 1994; Griffith et al. 1999b).

For intersexual signals, variation in the environmental conditions experienced is known to be an important source of variation in signal form and function within species. For example, signal variation may be driven by differences in the efficacy of signal transmission between habitats (Endler & Houde 1995) or by differences in predation pressures (Endler 1980). Divergent selection on traits correlated with the signalling trait can also drive variation in signal form: in cases where the strength and/or direction of selection on correlated traits varies across environments, the form of the signal, as well as the underlying variation in the signalling trait, may therefore also vary (Wilczynski & Ryan 1999). Additionally, where signal expression is dependent on individual condition, differences in the availability of resources can also drive changes in signal expression between populations (Hill 1994; Grether et al. 1999). Finally, studies have indicated that genotype-by-environment interactions can maintain variation in signalling traits and in receiver responses to those traits via differences in the relative fitness of genotypes across environments (Griffith et al. 1999b; Qvarnström 1999).

In the case of intrasexual signals, however, much less is known about the role of the environment in generating variation in signalling between populations. Intrasexual traits may also show condition-dependence (Tibbetts & Curtis 2007) and their development can be sensitive to variation in environment al conditions (Griffith et al. 1999a; Mysterud et al. 2005). In addition, the efficacy of signal transmission can depend on prevailing environmental conditions (Wong et al. 2007). Together, these features indicate that the signal value of intrasexual traits may also vary in response to the environment, in a manner similar to that observed for intersexual traits. Given that intrasexual signalling represents an important adaptation to competition in many species (Maynard Smith & Harper 2003), identifying the causes and consequences of variation in intrasexual signals are important steps in understanding how sexual selection and environmental factors interact to determine the dynamics of competition in the wild.

In this study, we explore potential environmental factors driving inter-population variation in intrasexual signalling in the paper wasp *Polistes dominulus*. *P. dominulus* is a temperate species with a widespread distribution, having undergone several major expansions in recent years from its native range in Africa and Eurasia into North America, South America and Australia (Liebert et al. 2006). In the northeastern United States, Tibbetts and co-workers have provided evidence for the use of an intrasexual (status) signal during competition between females, based on melanin patterning on the clypeus (Tibbetts & Dale 2004; Tibbetts & Lindsay 2008). Clypeal patterning is fixed throughout adult life and varies among females from a completely yellow clypeus (i.e. no black spots) to black spots of variable size and shape (Tibbetts & Dale 2004). Previous work has argued that the active signalling component of the clypeal pattern is not the presence or size of the black spots, but rather the degree of disruption or 'brokenness' (*sensu* Tibbetts & Dale (2004)) in the pattern (Tibbetts & Dale 2004; Tibbetts 2010). However, brokenness is tightly linked to the amount of black on the clypeus: individuals lacking black clypeal spots have a brokenness score of zero, whereas nearly all individuals with black spots have a brokenness score greater than zero, with brokenness increasing as a function of the number and/or waviness of the black spots (Tibbetts & Dale 2004; Tibbetts 2006; Fig. 1). Variation in brokenness within a population thus crucially depends on the variability in the amount of black on the clypeus among wasps.

Recently, studies of *P. dominulus* populations in other geographical locations have reported striking differences in clypeal patterning at the population level (Cervo et al. 2008; Zanette & Field 2009; Tibbetts et al. 2011). In Hungary, Ukraine and the northeastern USA, variability in the amount and distribution of black on the clypeus is high, and around 80% of wasps have black clypeal spots of varying size and shape (Tibbetts & Dale 2004; Rusina et al. 2006; Tibbetts 2006; Tibbetts et al. 2011; J. P. Green & Z. Ács, unpubl. data). As a result, average brokenness within these populations is high (Tibbetts

Fig. 1: Portraits of four *Polistes dominulus* females (spring foundresses) collected in southern Spain in 2008–2009, arranged in order of increasing brokenness of the clypeal pattern from a–d. Importantly, variation in brokenness among females depends upon variation in the amount of black on the clypeus: females lacking clypeal spots have a brokenness score of 0, whereas the vast majority of females with clypeal spots have a brokenness score >0, which increases with the number and/or waviness of the spots (see main text).

et al. 2011). In contrast, in Italy and Spain, variability in clypeal patterning is much lower, with as many as 80% of wasps having a completely yellow clypeus (Cervo et al. 2008; Zanette & Field 2009). As a consequence, average brokenness within these populations is much lower (Tibbetts et al. 2011). Interestingly, these population differences in pattern variability and brokenness are associated with differences in the signal value of clypeal patterns. In the US, where pattern variability and brokenness are high, brokenness signals fighting ability to rivals; in Spain, however, where pattern variability and brokenness are low, brokenness has no signal value during competition (Green & Field 2011). Variation in the use of the clypeal pattern as a signal between the US and Spain may therefore be due to differences in variability in brokenness between populations (Green & Field 2011; Tibbetts et al. 2011).

In a recent study exploring the factors responsible for the variation in clypeal patterning between populations, Tibbetts et al. (2011) noted an apparent association between clypeal patterning and climate, with wasps in cooler habitats tending to have more clypeal spots and thus a higher brokenness (Tibbetts et al. 2011; Fig. 2). Climatic effects on the development of melanin patterning have been described in a variety of insect species (e.g. Tsuruta et al. 1989; Goulson 1994; Parkash et al. 2008), and polymorphism in melanin patterning among wild insect populations often reflects local adaptation to prevailing climatic conditions (reviewed in True 2003; Nijhout 2010). Climate may thus play an important role in driving differences in clypeal patterning between *P. dominulus* populations and may ultimately account for the variation in the signal value of the clypeal pattern among populations. However, the data presented by Tibbetts et al. (2011) do not permit a rigorous test of this hypothesis, and a manipulation is required to test directly the impact of climate on the expression of the *P. dominulus* clypeal pattern.

Here, we explore whether variation in climatic conditions drives variation in clypeal patterning in *P. dominulus*. In an early study of *Polistes* colouration, Enteman (1904) reared pupae from a single nest of *Polistes fuscatus* (ex *Polistes variatus*) in different temperature and humidity regimes. Her results suggested that there might be effects of both factors on the extent and degree of melanisation in the resulting adults. In this study, we aimed to test for effects of climatic factors on the expression of clypeal patterns in *P. dominulus* using a similar experimental design on a larger scale. We housed pupae from the same nests under four different combinations of temperature and humidity and compared the brokenness of adult females emerging under each of the four conditions.

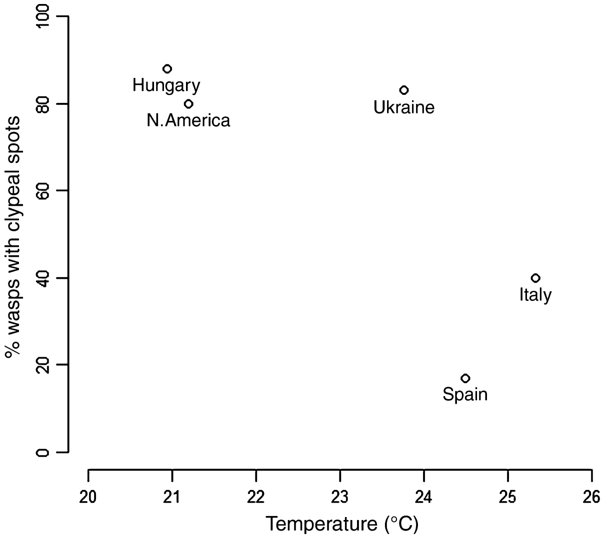

Fig. 2: Proportion of *Polistes dominulus* females with clypeal spots in relation to ambient temperature (°C) during the period of late worker and reproductive development across five geographical areas. Data represent mean daytime temperatures for June–July (Spain) and July–Aug. (Hungary, Italy, North America, Ukraine) over a 10-yr period (2001–2010). Clypeal pattern and colony cycle data from: Hungary (J. P. Green & Z. Ács, unpubl. data); Italy (Queller et al. 2000; Cervo et al. 2008); North America (Tibbetts & Dale 2004); Spain (Zanette 2007; Leadbeater et al. 2011); Ukraine (Rusina et al. 2006). Temperature data obtained from the following weather stations: Florence 161700 (Italy), Ithaca, NY 725155 (North America), Jerez 84510 (Spain), Kherson 339020 (Ukraine) and Veszprem 128300 (Hungary). Data accessed at www.tutiempo.net/en/.

Methods

Study population

We collected *P. dominulus* nests from farmland near Conil de la Frontera, Cádiz Province, Spain (36°15′35″N, 06°04′11″W, 35 m a.s.l.) where wasps build nests on sunlit patches of prickly pear cactus (Shreeves et al. 2003). In our population, nests are founded in late Feb.–early Mar. by lone females (foundresses) or by groups of co-foundresses. The first offspring emerge in late Apr.–May; the majority of these offspring are females that remain on the nest as workers. Offspring continue to emerge until the end of the season (mid-July), at which point surviving offspring disperse to mate. Mated females (gynes) then overwinter to found nests in the following spring. We collected 20 large nests in early June 2010 in the reproductive stage of the colony cycle, when the majority of emerging females will leave the nest to mate and overwinter

(Leadbeater et al. 2011). In a recent study, Tibbetts et al. (2011) reported variation in clypeal patterning between workers and gynes. By selecting only reproductive-destined individuals for the rearing experiment, we sought to minimise this natural source of variation in clypeal patterning. Nests were collected by gently removing them from the cactus using forceps so as not to tear the nest or damage the brood and placing them in zip-lock bags (adults were not collected).

Rearing experiment

We performed the rearing experiments at the University of Sussex, UK. We divided nests into four pieces, each piece of roughly equal size and containing a variable number of pupae (5–44, mean ± 1 SD = 16.2 ± 7.8). We placed nest quarters individually in small plastic pots (4 × 4 × 6 cm), with wire mesh over the top, and housed them in identical SANYO MR350 growth chambers (52 × 49 × 113.5 cm; SANYO E&E Europe BV, Loughborough, UK). The development of melanin patterning in some insect species is sensitive to light/photoperiod (Nijhout 1999). To control for any effects of light on clypeal pattern development, we kept nests in constant darkness. Each nest quarter was reared under one of the following four temperature–humidity regimes: 20°C/40% RH, 20°C/65% , 30°C/40% RH and 30°C/65% RH. In 2010 at the Spanish field site, ambient conditions during the reproductive phase of the colony cycle (June–July) ranged from 12 to 37°C and from 34% to 87% RH [Jerez weather station (84510); www.tutiempo.net/en/]. The levels of humidity and temperature used in the rearing experiment were thus within the natural range experienced in the wild.

We collected all wasps eclosing over the course of the experiment. However, morphological measurements were taken from females eclosing only 7 d or more after the start of the experiment, to ensure that they had been exposed to the experimental conditions for a reasonable portion of their development, which typically lasts around 19 d in the wild (E. Leadbeater & J. Field, unpub. data). Thereafter, we collected newly eclosed females at regular intervals (every 2 d) for three weeks, after which point no more wasps emerged. Males were not collected for analysis as they do not have variable clypeal patterns. Parasitoids [*Latibulus argiolus* (Rossi)] emerging on 18 nests were also discarded.

After collection, wasps were killed by freezing. We removed the head of each wasp using a scalpel and took a photograph of the clypeus using a Nikon D80 digital camera (with macro lens) (Nikon UK Ltd, Surrey, UK). We calculated brokenness for each female in MATLAB v. 7.1 (The MathWorks Ltd., Cambridge, UK) following the method described in Tibbetts (2010). Briefly, digital images of the clypeus were converted into a standard 60 × 30 pixel bitmap. Brokenness was then calculated as the standard deviation of the number of black pixels in each vertical column of the bitmap from pixels 6 to 55 along the horizontal gradient of the clypeus. Pixels 1–5 and 56–60 were excluded as these contained black pixels corresponding to the border of the clypeus, rather than to the patterns on the clypeus (Tibbetts 2010). We also recorded the dry weight of each wasp (minus the head) as brokenness and body size have been shown to be positively correlated in some populations (Tibbetts et al. 2011). Wasps were weighed following drying in an oven at 60°C for 8 d using a balance accurate to 0.0001 g.

Statistical analyses

All analyses were performed in R v. 2.14.2 (R Development Core Team 2011). Research by Tibbetts (2010) has demonstrated a heritable component in the amount of black on the clypeus in a *P. dominulus* population in the US. This finding indicates that clypeal patterns may be more similar among females emerging on the same nest (who are often sisters) than between females on different nests. A comparison of the proportion of wasps eclosing on each nest with clypeal spots confirmed that there was significant between-nest variation in clypeal patterning (GLM, $\chi^2_{19} = 67.79$, $p < 0.0001$). Data were therefore analysed using linear mixed models (LMM; 'nlme' library) and generalised linear mixed models (GLMM; 'cplm' and 'lme4' libraries), in which 'nest' was fitted as a random factor to control for similarities in clypeal patterning among wasps from the same nest. In all analyses, model simplification proceeded by backwards deletion of non-significant terms until further removals led to significant ($p < 0.05$) increases in deviance, assessed using log-likelihood tests for LMM and chi-squared values for GLMM. Significance levels are reported on the addition of non-significant terms and removal of significant terms from the minimum adequate model.

Results

Climatic effects on clypeal pattern brokenness

We collected morphological data for 223 females eclosing within the collection period [mean number of females per nest (±1 SD) = 11.15 ± 7.13]. We tested whether climate affected the brokenness of the clypeal pattern using a GLMM with Tweedie errors, which are suitable for modelling continuous, zero-inflated data (here, zero-inflation results from the large number of individuals without clypeal spots, each of whom consequently have a brokenness score of zero). Temperature, humidity, body weight and all two-way interactions were included as explanatory variables. The analysis revealed a highly significant effect of temperature on brokenness. Wasps eclosing at 20°C had a higher pattern brokenness than those at 30°C ($\chi^2_1 = 27.58$, $p < 0.0001$; Fig. 3). However, there was no effect of humidity on brokenness, either directly ($\chi^2_1 = 0.59$, $p = 0.44$) or via an interaction with temperature ($\chi^2_2 = 1.03$, $p = 0.60$). There was also no effect of body weight on brokenness, either directly ($\chi^2_1 = 0.08$, $p = 0.77$) or via an interaction with temperature ($\chi^2_2 = 0.73$, $p = 0.70$) or humidity ($\chi^2_3 = 1.14$, $p = 0.77$).

Pupae housed at 20°C emerged with a higher brokenness than those at 30°C, which may indicate an effect of temperature on the brokenness of the clypeal pattern. However, this could also be due to an effect of temperature on the presence of clypeal spots. Wasps emerging at 20°C were 68% more likely to have clypeal spots than those at 30°C (GLMM, ($\chi^2_1 = 16.71$, $p < 0.0001$). Given that wasps with clypeal spots almost always have a higher brokenness than those without spots (see Introduction), a higher brokenness among wasps at 20°C may simply be a consequence of the higher proportion of wasps with clypeal spots. To address this possibility, we repeated the above-mentioned analysis for the subset of wasps with clypeal spots ($n = 76$) using an LMM with brokenness (log-transformed) as the response variable and temperature as the explanatory variable. The analysis revealed that, among wasps with clypeal spots, brokenness was significantly higher among wasps emerging at 20°C than at 30°C ($L_1 = 9.49$, $p = 0.002$).

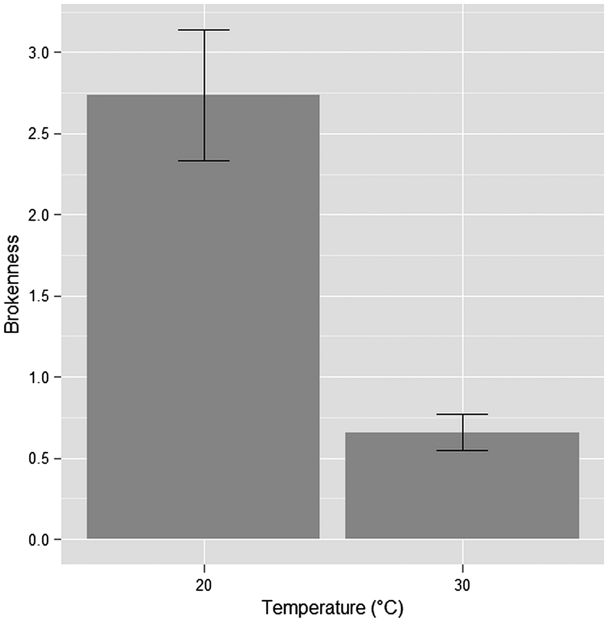

Fig. 3: Brokenness for wasps emerging at 20 and 30°C (means are shown ±1 SE).

Developmental plasticity vs. differential survival

The higher brokenness of wasps eclosing at 20°C provides support for the idea that temperature experienced during development affects the expression of the clypeal pattern. However, a similar result would be expected if wasps with more broken patterns showed enhanced survival at 20°C (e.g. because they are of higher quality; Tibbetts et al. 2011). Survival was generally low under all conditions, most likely due to damage sustained to the brood when transporting and quartering the nests. To test whether wasps with more broken patterns show enhanced survival at 20°C, we would ideally compare the survival of wasps with high and low brokenness. However, clypeal patterns are expressed only a few days before eclosion (J. P. Green, own data), meaning that it is impossible to determine clypeal patterning for any pupae that died before this time. Nonetheless, if conditions at 20°C imposed a bottleneck on survival, we would expect to see reduced survival among all wasps at 20°C compared with wasps at 30°C. We found no strong evidence for this: while the proportion of wasps surviving to eclosion was slightly lower at 20°C than at 30°C (47% vs. 52%), this difference was not significant (GLMM, $\chi^2_1 = 2.81$, $p = 0.09$).

A second way of determining whether the higher brokenness among wasps emerging at 20°C is because of enhanced survival of wasps with broken patterns is to test whether these wasps also differ in other characters linked with quality. Previous research suggests that body size may be a predictor of quality in *P. dominulus* (e.g. Turillazzi & Pardi 1977). We therefore tested whether among wasps emerging at 20°C those with more broken patterns were also heavier using an LMM with weight as the response variable and brokenness as the explanatory variable. The analysis revealed no significant relationship between weight and brokenness ($L_1 = 0.72$, $p = 0.40$). However, a second analysis of body weight across all wasps showed that wasps emerging at 30°C were significantly heavier than wasps emerging at 20°C (LMM, $L_1 = 14.51$, $p = 0.0001$).

Discussion

Identifying the causes of variation in sexually selected traits is crucial to understanding how such variation is preserved in the face of sexual selection. Here, we show that the expression of an intrasexually selected trait whose signal value varies between populations depends on thermal conditions during development. Wasps from the same natal nest reared in cooler conditions had more broken clypeal patterns than those reared in warmer conditions, even when controlling for similarities between wasps eclosing on the same nest. Enhanced survival and/or growth of wasps with more broken patterns in cooler conditions is unlikely to explain our result. Although survival was slightly lower at 20°C than at 30°C, this difference was not significant. Additionally, among wasps emerging at 20°C, those with highly broken clypeal patterns were not heavier than those with less broken patterns. Thus, the difference in patterning between temperature conditions is consistent with phenotypic plasticity in the development of the clypeal pattern in response to temperature.

Across *P. dominulus* populations, there is substantial variation in clypeal patterning, with wasps inhabiting cooler habitats more likely to have black clypeal spots and thus a higher brokenness (Tibbetts et al. 2011; Fig. 2). Our result suggests that this correlation is not incidental but that differences in the thermal environment during development could account for it. Recently, Tibbetts et al. (2011) have proposed that differences in brokenness between populations may be maintained by selection on body size, based on positive correlations between size and brokenness in populations in Italy and the USA (Tibbetts et al. 2011; but see Cervo et al. 2008). According to this hypothesis, higher brokenness in populations living in cold conditions arises as a consequence of selection for larger body size in habitats where food availability is low or unpredictable (Tibbetts et al. 2011; see also Chown & Gaston 2010). Our results offer little support for this hypothesis. Surprisingly, we found that body weight was lower, not higher, among wasps reared in cooler conditions. This is the opposite trend to that seen in many insects (Nylin & Gotthard 1998), including a second *Polistes* species, *Polistes gallicus* (ex *foederatus*) (Turillazzi & Conte 1981), although a positive trend between developmental temperature and body size has been described in a number of species (Nylin & Gotthard 1998; and references therein). More importantly, we found no correlation between brokenness and body weight, which is consistent with previous findings in other European populations (Cervo et al. 2008; Tibbetts et al. 2011). Together, these findings indicate that selection on body size is unlikely to drive variation in patterning between populations, although we are cautious about making inferences about patterns of selection across populations based on results from a single population (see Stillwell 2010). Moreover, it is possible that other aspects of condition potentially correlated with clypeal patterning (e.g. body fat content) are under selection in colder environments and that this helps to maintain variation in patterning between populations (Tibbetts et al. 2011 and references therein).

As we note earlier, our results indicate that expression of the clypeal pattern is plastic in response to temperature. Such plasticity may be adaptive if the benefits associated with producing a particular kind of pattern vary with climate. The negative trend between temperature and the proportion of individuals with clypeal spots in *P. dominulus* mirrors that in other insect species where melanin patterns play a role in thermoregulation. In these species, individuals living at high altitudes or latitudes show greater body melanisation, which permits more rapid heat absorption under cold conditions (True 2003). Furthermore, melanin patterning in many of these species exhibits plasticity in response to environmental cues, including temperature or associated cues such as development time (e.g. Goulson 1994; Marriott & Holloway 1998). Selection for efficient thermoregulation may account for the variation in patterning between *P. dominulus* populations. However, the amount of black on the clypeus is typically <1% of the total amount of black on the body cuticle (Tibbetts & Dale 2004), and it remains to be shown whether wasps with highly broken patterns also have more black on the body as a whole.

To understand in more detail why clypeal patterning varies between populations, we need to know more about how the pattern develops. While there is evidence that pattern development is influenced by larval nutrition (Tibbetts & Curtis 2007; Tibbetts 2010) and temperature (this study), the physiological mechanisms governing development remain to be explored. Studies of colour pattern formation in insects have shown that patterns arise as a consequence of complex effects of hormones on gene expression, the timing and intensity of which may be modulated by environmental factors (Nijhout 2010). Knowledge of these processes would yield valuable insights into the way in which clypeal patterning develops. For example, are there two distinct processes governing development, one determining the presence/absence of melanin and the other determining the specific arrangement of pigment, or is brokenness determined along a continuous gradient, ranging from no black spots to several spots of varying sizes and shapes? This is important to establish, as it has profound implications for how selection can act on elements of the pattern. For example, do elements of the pattern represent discrete polyphenisms, with the potential for selection to act on a distinct developmental switches (e.g. spot or no spot) (Nijhout 1999) or can they be modelled as reaction norms, varying continuously along different environmental gradients (Stearns 1989)?

Our finding that temperature affects the expression of *P. dominulus* clypeal patterns offers a potential explanation for the variation in signalling within this species. The observation that signalling via clypeal patterns is restricted to populations where pattern variability is high suggests that the amount of variation in patterning may constrain signal function. Environmental factors favouring reduced patterning may therefore effectively preclude signalling via brokenness in some populations. In Spain, high temperatures selecting for reduced patterning could account for the absence of signalling in this population. Conversely, in the USA, cooler temperatures during development could facilitate signal use via an increase in pattern variability. From previous studies, we know that environmental factors can constrain variation in sexual signals (e.g. Grether et al. 1999) and that the requirement for thermoregulation in particular can constrain selection on colour-based signalling (Lindstedt et al. 2009). In *P. dominulus*, climate-driven variation in the amount and distribution of melanin on the clypeus may maintain variation in the signal value of patterns between populations. A good test of this hypothesis would be to compare the signal value of clypeal patterns between other locations, for example, in Italy and Hungary, where pattern variability is low (Cervo et al. 2008) and high (Tibbetts et al. 2011), respectively.

In *P. dominulus*, the evidence presented here and elsewhere (Green & Field 2011; Tibbetts et al. 2011) indicates that there is geographical variation in the use of status signals between populations and that expression of the signal is affected by temperature, which potentially acts to constrain signal variability in some environments. Developmental sensitivity of intrasexual traits to environmental conditions has been demonstrated before (Griffith et al. 1999a; Mysterud et al. 2005). However, ours is the first study to demonstrate an effect of environment on an intrasexual trait whose signal value varies intraspecifically. This result suggests that differences in abiotic factors between habitats and populations may represent an important constraint on sexual selection for intrasexual traits and that the dynamics of competition between members of a species may vary in response to prevailing environmental conditions. Moreover, our result indicates that this variation need not be the result of environmental effects on individual condition or genotype x environment interactions but could instead be the result of plastic responses to local environmental conditions acting to constrain signal expression (e.g. Lindstedt et al. 2009). Indeed, as appears to be the case in *P. dominulus*, entire signalling systems may be present or absent from populations depending on variation in environmental conditions.

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