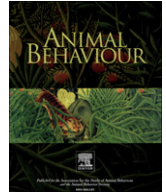




Contents lists available at ScienceDirect

## Animal Behaviour

journal homepage: [www.elsevier.com/locate/anbehav](http://www.elsevier.com/locate/anbehav)Interpopulation variation in status signalling in the paper wasp *Polistes dominulus*

Jonathan P. Green\*, Jeremy Field

School of Life Sciences, University of Sussex

## ARTICLE INFO

## Article history:

Received 5 August 2010  
 Initial acceptance 26 August 2010  
 Final acceptance 28 September 2010  
 Available online xxx  
 MS. number: 10-00528R

## Keywords:

competition  
 Europe  
*Polistes dominulus*  
 RHP  
 signalling  
 status badge  
 variation

Contests between individuals over resources may be costly in terms of both time and energy expended and the risk of injury. Signals of status, or 'status badges', are thought to have evolved to minimize these costs by providing information about an individual's fighting ability or resource-holding potential (RHP) at the start of a contest. Studies on recently established North American populations of the paper wasp *Polistes dominulus* have demonstrated the existence of a status badge, in the form of black clypeal patterns, and have shown that rivals attend to these patterns during competitive interactions. However, observational data from studies in this wasp's native European range have failed to demonstrate a strong link between clypeal patterning and RHP. We undertook the first direct test of status signalling in a European population of *P. dominulus*, by testing receiver responses to clypeal pattern manipulations in a competitive foraging context. We found no evidence that individuals assessed rivals using the clypeal 'badge'. We discuss possible reasons for variation in signal use between the American and European populations, including genetic drift and environmental effects of the development and transmission of the signal.

© 2010 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Contests between individuals over resources can inflict significant costs on both contestants, in terms of time, energy and the risk of injury or death. Theory suggests that the costs of escalated conflicts will be minimized if individuals can assess the competitive ability of their opponents at the start of contests, and thereby predict the likely outcome of a fight (Maynard Smith & Harper 1988). Conventional signals (otherwise known as status signals, or 'status badges') have been argued to play a role in resolving contests over relatively low-value resources, where the fitness payoffs of acquiring the resource are less than the fitness costs of escalated fighting (Rohwer 1975; Maynard Smith & Harper 1988). Visual status signals are small patches of colour that convey information about an individual's competitive ability, or resource-holding potential (RHP), to an opponent. These signals are 'conventional' in the sense that they are not causally linked to RHP, and are furthermore considered to be relatively cost free to produce, in contrast to indices and strategic signals (Maynard Smith & Harper 2003).

Status signals have attracted much controversy on both theoretical and empirical grounds over the issue of how signal reliability is maintained (reviewed in e.g. Senar 1999; Whiting et al. 2003). Explanations for the reliability of cheap, arbitrary status signals have largely focused on costs incurred during social interactions, which

act to prevent cheating (Senar 1999; Tibbetts & Dale 2004). Scenarios for these 'social costs' rely on the fact that escalated fighting is most likely between rivals each signalling at a high intensity (Whiting et al. 2003). For example, a dishonest signaller that attempted to extricate itself from an escalated conflict might be punished if an opponent detected the incongruence between its advertised status and its submissive behaviour (Rohwer 1977; Senar 1999).

Empirical support for status signalling has come largely from studies of passerines (e.g. Qvarnström 1997; Senar & Camerino 1998) and lizards (Whiting et al. 2003). Recently, however, a number of studies suggest that status signalling also operates in the paper wasp *Polistes dominulus* (Tibbetts & Dale 2004; Tibbetts & Lindsay 2008; Tibbetts et al. 2010). *Polistes dominulus* is a primitively eusocial species which lacks morphological castes. It has a cosmopolitan distribution, following recent expansions from its native Eurasian range into North and South America and Australia (Cervo et al. 2000). Nests are founded in the spring, either by lone foundresses or by groups of cofoundresses, all of which are inseminated and can potentially lay eggs. In cofoundress groups, egg laying is determined by rank within a linear hierarchy that emerges during nest founding, with dominant (Rank 1) females monopolizing reproduction. In North American populations, patterns of melanin on the clypeus are argued to signal status in both dominance (Tibbetts & Dale 2004) and competitive interactions (Tibbetts & Lindsay 2008; Tibbetts et al. 2010). The active signal component, 'brokenness' (a measure of pattern disruption; Tibbetts 2010), has been shown to be a reliable signal of RHP, with social costs enforcing honesty (Tibbetts & Dale

\* Correspondence: J. P. Green, School of Life Sciences, JMS Building, University of Sussex, Falmer, Brighton BN1 9QG, U.K.

E-mail address: [j.p.green@sussex.ac.uk](mailto:j.p.green@sussex.ac.uk) (J.P. Green).

2004). However, two studies in the species' native Eurasian range have failed to find evidence of a strong correlation between pattern brokenness and hierarchical rank in spring foundress groups (Cervo et al. 2008; Zanette & Field 2009). Cervo et al. (2008) were also unable to demonstrate a link between clypeal patterning and survival and health. These findings cast doubt on the function of clypeal patterns as badges of status in European populations and indicate that there may be geographical variation in status signalling in *P. dominulus*. However, support for this hypothesis requires a manipulative test of status signal use in Europe, which to date has been lacking.

In this study, we tested for status signalling in the Spanish population of *P. dominulus* studied by Zanette & Field (2009). In testing for a signal function in the clypeal pattern, we followed the experimental procedure of Tibbetts & Lindsay (2008). The demonstration of status signalling requires that manipulation of the putative signal should result in a change in behaviour in the receiver, consistent with the idea that the signal conveys information about individual RHP. This is not straightforward, for two reasons (Senar 1999). First, a change in receiver behaviour may be caused by difficulties with individual recognition following manipulation of the signaller (Shields 1977). Second, studies using familiar individuals run the risk of confounding the demonstration of status signalling with the demonstration of anticheating mechanisms, which may interfere with receiver responses if the signaller's true status is known to the receiver (Senar 1999). It is important, therefore, that the receiver has not interacted with the signaller prior to the manipulation, and that the receiver possesses no information about the signaller's RHP, other than what is signalled. The design used here and by Tibbetts & Lindsay (2008) fulfils these requirements: focal wasps were presented with a choice of two food sources, each guarded by a potential rival with artificially enhanced or reduced clypeal patterns. These 'guards' had not previously interacted with the focal wasps. Furthermore, the guards were presented dead to prevent focal wasps detecting any incongruence between behaviour and advertised status. If wasps do use clypeal patterns to assess rivals in a contest situation, we expected to see focal wasps avoiding the high-status guard, and instead preferring to challenge the low-status guard for access to food, as seen in Tibbetts & Lindsay (2008).

## METHODS

Protocols followed Tibbetts & Lindsay (2008). Wasps were collected in early May 2010 at sites around Conil de la Frontera (Cádiz Province, Spain). All wasps were spring foundresses from different nests in the pre-emergence phase of the colony cycle. Guards and focal wasps were collected from sites at least 3 km away to minimize the likelihood of previous interaction. Wasps were transferred to large plastic containers (25 × 16 cm and 16 cm high) where they were held for 48 h, and provided with ad libitum water and sugar cubes. Focal wasps and guards were housed in separate containers. Wasps were then placed individually in plastic tubes and starved for 24 h prior to trials.

Trials were carried out in a rectangular arena (6 cm wide × 7 cm long) with a convex semicircle at one end. At the other end, a sugar cube with a freeze-killed 'guard' wasp on top was placed in each corner. Guards were matched by size (within 0.1 mm wing length) and by the number of clypeal spots; care was taken to select guards of intermediate wing length (range 10.39–12.39 mm), thereby avoiding very large or very small guards. The active signalling component of the pattern is argued to be the amount of disruption, or 'brokenness' (Tibbetts 2010); however, when manipulating patterns, previous studies have altered the number of facial spots, as this is a good proxy for brokenness (Tibbetts & Lindsay 2008). One guard of each pair was painted with Testor's enamel paint to

signal a higher status while the other guard was painted to signal a lower status. We used three combinations of guard facial patterns. Wasps with no spots were painted to produce guards with one and two spots, respectively. Wasps with one spot were painted to produce guards with no and two spots, and wasps with two spots were painted to produce guards with no and one spot. A total of 13 individual pairs of guards were used in 149 trials.

Focal wasps were placed within a covered tube at the semicircular end of the arena for 5 min prior to the trial. Wasps were then released into the arena and their choice of sugar cube recorded. We considered the wasp had made a choice when it approached a sugar cube and began to eat. Wasps were given 30 min to make a choice; the median time from release until eating was 50 s (range 2 s–28 min). Fresh sugar cubes were added at the start of each trial.

Previous research has suggested that, when choosing between guards, wasps use information about their own RHP in addition to information about guard RHP (Tibbetts et al. 2010). For example, focal wasps with more clypeal spots showed no preference when presented with guards with no or one spot (Tibbetts et al. 2010). To control for potential effects of focal wasp quality on guard choice, all focal wasps used in the trials had the same number of clypeal spots (i.e. none). We chose to use no-spot individuals as focal wasps in the trials as they represent the most frequent clypeal pattern type in our population (see Discussion), thus permitting a large sample size in the experiment.

## Statistics

All analyses were performed using the software R version 2.9.2 (<http://www.r-project.org/>). We tested whether wasps preferred to challenge the high-spot or low-spot guards using a Pearson chi-square test. To test the effect of specific pairings of guard facial patterns (i.e. no versus one spot, no versus two spots and one versus two spots) on wasps' choices, we used a generalized linear mixed model with binomial errors. Wasp choice was the binary dependent variable (0 = low-spot guard; 1 = high-spot guard) and guard facial pattern pair was the explanatory variable. Although guards were matched for size, we included guard size as a second explanatory variable to test whether small differences in size influenced guard choice. Whether the chosen guard was in the left or right corner of the arena was also included as an explanatory variable. Finally, individual guard pair was added to the model as a random effect to control for similarities within guard pairs in terms of focal wasp choice. Model simplification proceeded by backwards deletion of nonsignificant terms until further removals led to significant ( $P < 0.05$ ) increases in deviance. Significance levels are reported on the addition of nonsignificant terms, and removal of significant terms, from the minimal adequate model.

## RESULTS

Our main finding was that focal wasps did not challenge the low-spot guard significantly more often than the high-spot guard (Pearson chi-square test:  $\chi^2_2 = 1.71$ ,  $P = 0.43$ ; Table 1). Furthermore, the same result was obtained when we considered only trials in which focal wasps chose between no- and one-spot guards or

**Table 1**  
Numbers of focal wasps choosing to challenge high-spot and low-spot guards

Guard facial pattern (no. of spots)	Low-spot guard	High-spot guard
0 versus 1	4	4
0 versus 2	18	14
1 versus 2	19	27
Total	41	45

between no- and two-spot guards (Pearson chi-square test with Yate's correction:  $\chi^2_2 = 0.01$ ,  $P = 0.94$ ). This indicates that the lack of preference for the low-spot guard was not the result of a specific failure to choose between one- and two-spot guards, which might be expected if mutual assessment is occurring (i.e. no-spot focal wasps might not be motivated to choose between one- and two-spot guards, if both represent superior competitors). Rather, our results demonstrate a general failure to choose between guard facial patterns, irrespective of the specific combination of guards.

Analysis of factors influencing the focal wasp's choice of the low-spot or high-spot guard showed no influence of guard position in the arena on focal wasp choice ( $\chi^2_1 = 1.15$ ,  $P = 0.28$ ). The analysis, however, revealed a significant interaction between the guard facial pattern pairing and guard size ( $\chi^2_2 = 31.01$ ,  $P < 0.001$ ). When presented with guard pairs with either no and one spot or no and two spots, wasps that chose the smaller guard were more likely to choose the guard with more spots. However, this tendency was not observed among wasps choosing between guard pairs with one and two spots.

To analyse the effects of guard facial pattern and size on focal wasp choice in more detail, we ran a second model in which the interaction was omitted. In the absence of the interaction, neither guard facial pattern pairing nor size had a significant effect on focal wasp choice (facial pattern pair:  $\chi^2_2 = 1.52$ ,  $P = 0.47$ ; size:  $\chi^2_1 = 0.08$ ,  $P = 0.77$ ). Thus, when all guard pair types are considered, focal wasps showed no preference for either the smaller or larger guard. Similarly, when guard size is not considered, the focal wasps' choice of the low-spot or high-spot guard did not depend on the specific combination of facial patterns presented by the guard pair.

During the trials, 63 focal wasps did not eat at either sugar cube. To test whether the likelihood of eating (i.e. the likelihood of approaching either guard) was influenced by the particular combination of guard patterns, a second generalized linear mixed model was run. Decision to eat was the binary dependent variable, and guard facial pattern pairing and guard size were the independent variables. Guard size was taken as the size of the smallest guard in a pair. Individual guard pair was again added as a random effect. The analysis revealed no significant effect of either guard facial pattern pairing or guard size on the decision to eat (guard facial pattern:  $\chi^2_2 = 0.69$ ,  $P = 0.41$ ; guard size:  $\chi^2_1 = 0.05$ ,  $P = 0.83$ ). Furthermore, the interaction between guard facial pattern and size did not influence the probability of eating ( $\chi^2_2 = 0.34$ ,  $P = 0.57$ ). Therefore, the decision to approach either guard and eat the sugar was not influenced by the relative size of the guards or by the particular combinations of guard clypeal patterns (i.e. wasps were equally likely to eat when presented with pairs of guards with no versus one spot, no versus two spots or one versus two spots).

These results show that focal wasps did not prefer to challenge the low-spot guard. To exclude the possibility that this result is due to differences in experimental set-up (e.g. illumination), we conducted another set of trials in which wasps were given the choice between a sugar cube guarded by a no-spot wasp and an unguarded cube. If wasps can perceive the presence of a guard, then wasps should prefer to feed at the unguarded sugar cube to avoid competition. We found that wasps were significantly more likely to feed at the unguarded sugar cube (binomial test:  $N = 35$ , 69%,  $P < 0.05$ ). This result is important as it demonstrates that wasps perceive the presence of another wasp in our set-up, and so could use information about the guard's phenotype when choosing between guards.

## DISCUSSION

We found no evidence that wasps assess conspecifics via visual status signals in a foraging context. When given the choice of two food sources, one guarded by a high-spot guard and the other by

a low-spot guard, focal wasps did not show a preference for feeding near the low-spot guard. This suggests that the decision to challenge a particular rival is made without reference to the rival's clypeal patterns, in particular the number of clypeal spots. We also found that the decision to approach either guard (i.e. the decision to eat) was not influenced by particular combinations of guard facial patterns. We observed a significant interaction between guard size and the guard facial pattern type, although this is difficult to interpret in light of previous work. The finding that individuals choosing high-spot guards from certain pairings (no versus one spot or no versus two spots) tended also to choose the smaller guard could be seen as evidence for rival assessment, with individuals attempting to minimize competition by choosing opponents of smaller size when facial patterns indicate high status. However, it is not clear why these effects are seen only in these pairs of guard facial patterns, and not in the choice trials involving one- and two-spot guards. In the absence of any interaction, the specific combination of guard facial pattern did not influence focal wasp choice, consistent with the idea that relative differences in signal intensity (i.e. brokenness, or number of spots), rather than specific patterns, are important to the receiver when assessing rivals (Tibbetts & Lindsay 2008).

Our finding that clypeal patterns are not involved in rival assessment contrasts with that of Tibbetts & Lindsay (2008), who have found evidence for status signalling in a North American population of the same species. In the same set-up as used in the present study, Tibbetts & Lindsay (2008) demonstrated a strong preference for feeding near the low-spot guard. Preference for the low-spot guard was observed regardless of the specific combinations of guard facial patterns, suggesting that focal wasps discriminated between rivals based on facial patterns in general, rather than showing preference for, or avoidance of, a particular pattern (Tibbetts & Lindsay 2008). Furthermore, in a second choice experiment, Tibbetts et al. (2010) again demonstrated a preference for feeding near the low-spot guard, although this preference was dependent on the facial pattern of the focal wasp (Tibbetts et al. 2010). Taken together, these findings suggest that, in North American populations of *P. dominulus*, foundresses attend to clypeal patterns during social interactions and behavioural responses are determined, at least in part, by asymmetries in clypeal patterning between rivals.

This study represents the first explicit test of status signalling in a population of *P. dominulus* in its native European range. Given the number of studies furnishing empirical support for status signalling in *P. dominulus* (Tibbetts & Dale 2004; Tibbetts 2008; Tibbetts & Lindsay 2008; Tibbetts & Shorter 2009; Tibbetts et al. 2010), it is perhaps surprising that we failed to find evidence for status signals operating in our population. As we note above, the experimental set-up used for the choice trials closely resembles that used in previous studies. One difference, however, is the use of no-spot focal wasps, rather than the one-spot wasps used by Tibbetts & Lindsay (2008). No-spot wasps were used to maximize our sample size, as they represent the most common pattern type in our population (Zanette 2007). However, a potential concern with using no-spot wasps rather than one-spot wasps is that the two groups may behave differently if information about personal quality is also used in guard choice (Tibbetts et al. 2010). A previous study by Tibbetts et al. (2010) found that no-spot wasps showed no preference for one- versus two-spot guards: no-spot guards are considered to be of low quality, and are argued not to choose between opponents of higher quality (one- and two-spot guards). Although the no-spot focal wasps used in our experiment may not have discriminated between one- and two-spot guards for this reason, no-spot wasps using mutual assessment would still be expected to challenge the no-spot guard more often in the no- versus one-spot and no versus two-spot guard combinations. This is because a no-spot guard represents a more equal competitor (i.e. signals a similar RHP). Our finding that focal wasps do not prefer

to challenge the no-spot guard when present indicates that the lack of preference is not the result of strategic decisions using information on individual quality, but rather is consistent with the absence of visual status signalling in this population.

The level of motivation experienced by the focal wasps is a second factor that may account for the difference between the results from this study and those from previous studies. Tibbetts (2008) has shown that when hunger levels are increased, thereby increasing the value of the food source, wasps are more likely to challenge a high-spot guard. Could high hunger levels of focal wasps account for the absence of rival assessment in this study? Several aspects of our experimental design suggest that this is unlikely. First, focal wasps used in our experiment were starved for 24 h prior to the choice trials, the same starvation period experienced by wasps in Tibbetts & Lindsay's (2008) study. Prior to this period, wasps were provided with ad libitum sugar for 48 h: food reserves were therefore unlikely to be low before the starvation period. Although Tibbetts (2008) found that motivation to challenge a guard increased with increasing hunger levels, this effect was only observed when comparing wasps starved for 3 days and wasps given unrestricted food. Wasps starved for 24 h were not significantly more likely to approach the high-spot guard than wasps that had not been starved; they were not significantly quicker to approach the food source and did not spend longer eating (Tibbetts 2008). Although Tibbetts (2008) used one-spot focal wasps, there is currently no reason to believe that tolerance to starvation varies systematically with clypeal patterning, such that adults with more elaborate clypeal patterns are better able to withstand starvation. Indeed, the fact that, in our study, latency to eating was similar to that reported previously (median time to eating was 50 s versus 1 min in Tibbetts & Lindsay 2008) suggests that focal wasps were similarly motivated when presented with the choice task. The fact that a significant proportion of wasps tested did not approach the sugar after the starvation period also indicates that hunger levels in focal wasps were not too high to preclude rival assessment.

Finally, a third possible reason for the absence of a preference between guard facial patterns in this experiment may have been that the focal wasps were unable to see the guards. However, in a second experiment, wasps showed a significant preference for eating at the unguarded versus guarded sugar cube. This result indicates wasps were able to see guards and supports the assumption underlying the choice paradigm that wasps should prefer to feed wherever the risk of competition from conspecifics is lowest. Overall, we feel confident that our result is not an artefact arising from differences in experimental design. This points to a genuine difference in signal function between American and European populations: clypeal patterns do not appear to represent 'badges of status' in Spanish *P. dominulus*.

Our negative result is consistent with other observations on European populations of *P. dominulus* (Cervo et al. 2008; Zanette & Field 2009). Observing dominance interactions between cofoundresses on established nests, Cervo et al. (2008) found that neither the disruption ('brokenness') nor the size of the pattern differed significantly between Rank 1 and Rank 2. In a separate study, Zanette & Field (2009) explored the influence of clypeal patterns on social rank earlier in the pre-emergence phase of the colony cycle, before group composition had stabilized. Within cofoundress associations, the size of the clypeal pattern had a weakly significant effect on rank, with Rank 1 sporting a larger black mark than her subordinates. Although cited as evidence for an association between clypeal patterning and dominance (Tibbetts & Shorter 2009), Zanette & Field's (2009) results should be interpreted with caution. First, the effect of clypeal patterning was no longer significant when other potential determinants of rank were included in the regression (Zanette & Field 2009). Second, the study measured only the size of the clypeal mark, and did not quantify

pattern disruption (brokenness). Tibbetts (2010) has argued that the area of the pattern represents the nonsignalling component, while the active signalling component is the pattern's brokenness. An (weak) association between pattern size and rank would therefore say little about the potential for status signalling in the Spanish population. Indeed, among patterned wasps in this population, area and brokenness are not significantly correlated (J. P. Green & J. Field, unpublished data).

A striking feature of the Mediterranean populations is that clypeal pattern variability is much lower than has been reported for American populations. While 85% of wasps in the population investigated by Tibbetts & Dale (2004) show some clypeal patterning, only 40% of wasps in Italy (Cervo et al. 2008) and as few as 15% in Spain (Zanette 2007) have these patterns. An important consequence of this low variability in clypeal patterning is that its importance in mediating social conflict is necessarily limited. The presence of clypeal patterning is neither necessary nor sufficient for the acquisition of high rank, as demonstrated by Cervo et al. (2008) and Zanette & Field (2009). Furthermore, the majority of contests over resources such as food or reproduction will be between individuals without clypeal marks. Rival assessment based on clypeal patterning will therefore often fail to reveal differences in individual RHP in these populations. We suggest that the difference in prevalence of clypeal patterns between Mediterranean and American populations can be considered further evidence of genuine variation in signal use between these populations.

Geographical variation in the value of secondary sexual traits is well documented (Wilczynski & Ryan 1999; Dunn et al. 2008; Takahashi et al. 2008). However, most studies have focused on the value of intersexual traits (i.e. 'ornaments' used in mate choice), while there are few accounts of geographical variation in the value of intrasexual traits, including conventional (status) signals. One possible example of population divergence in status signalling comes from studies on the collared flycatcher, *Ficedula albicollis*, in Sweden (Pärt & Qvarnström 1997; Qvarnström 1997) and Hungary (Garamszegi et al. 2006). In Sweden, the forehead patch acts as a signal of status in territorial contests between males (Pärt & Qvarnström 1997; Qvarnström 1997), whereas in Hungary, territorial defence is not associated with forehead patch size (Garamszegi et al. 2006). The reason for this variation in plumage function is not currently understood, but in *F. albicollis* there is some evidence that the forehead patch is also a target of female choice (Gustafsson et al. 1995). In cases where status signals are additionally used in mate choice, variation in the signal phenotype could be explained by divergence in female preference for the trait, rather than changes in the intensity of intrasexual competition between populations.

In *P. dominulus* wasps, clypeal patterns are present only on females, and there is no evidence from observations of mating behaviour that males choose among females (Beani 1996). What then might account for variation in the frequency of clypeal patterns and their use as signals between populations? One factor promoting variation may be genetic drift, with populations passing through genetic bottlenecks during the first founding events in the U.S.A. 30–40 years ago (Cervo et al. 2000). There is evidence that the size of the clypeal mark is a heritable trait (Tibbetts 2010), suggesting that an initial difference in pattern prevalence may be preserved or even amplified over generations. However, the recent finding of relatively high genetic variability in American populations points to multiple independent founding events (Liebert et al. 2006), suggesting that bottlenecks may not have been particularly severe.

An alternative explanation could be that variation in pattern prevalence and function is due to environmental effects on the development of the clypeal pattern. Under the developmental conditions present in some environments, clypeal patterning may be prevalent/variable enough within the population to function as

a status badge, while conditions in other environments result in a less variable pattern. In particular, there is good evidence that climatic factors, such as temperature and humidity, affect the extent of melanin patterning in insects (Usui et al. 2004; Parkash et al. 2008), including *Polistes* wasps (Enteman 1904). Climate differences could therefore potentially explain the interpopulation variation in clypeal patterning in *P. dominulus*, with lower temperatures and/or higher humidity generating more variable clypeal patterns in populations at higher latitudes, as is seen in a number of bird species (Price 2006). This hypothesis is consistent with the greater pattern variability in New York State than in our southern Spanish population. Data on pattern variability and status signalling from other, more northerly, populations in the species' ancestral range would provide a clearer picture of possible climatic effects on pattern development and signal function.

### Acknowledgments

Thanks to Rosie Foster for help collecting wasps and setting up trials, Elli Leadbeater and Patrick Green for useful discussion and comments on the manuscript and the referees for comments. This research was funded by a GTA studentship from the University of Sussex (to J.P.G.) and a Natural Environment Research Council grant (to J.F.).

### References

- Beani, L. 1996. Lek-like courtship in *Polistes* wasps: 'a prolonged, delicate, and troublesome affair'. In: *Natural History and Evolution of Paper-wasps* (Ed. by S. Turillazzi & M. J. West-Eberhard), pp. 113–125. Oxford: Oxford University Press.
- Cervo, R., Zacchi, F. & Turillazzi, S. 2000. *Polistes dominulus* (Hymenoptera, Vespidae) invading North America: some hypotheses for its rapid spread. *Insectes Sociaux*, **47**, 155–157.
- Cervo, R., Dapporto, L., Beani, L., Strassmann, J. E. & Turillazzi, S. 2008. On status badges and quality signals in the paper wasp *Polistes dominulus*: body size, facial colour patterns and hierarchical rank. *Proceedings of the Royal Society B*, **275**, 1189–1196.
- Dunn, P. O., Whittingham, L. A., Freeman-Gallant, C. R. & DeCoste, J. 2008. Geographic variation in the function of ornaments in the common yellowthroat *Geothlypis trichas*. *Journal of Avian Biology*, **39**, 66–72.
- Enteman, W. M. 1904. *Coloration in Polistes*. Washington, DC: Carnegie Institution of Washington.
- Garamszegi, L. Z., Rosivall, B., Hegyi, G., Szöllösi, E., Török, J. & Eens, M. 2006. Determinants of male territorial behavior in a Hungarian collared flycatcher population: plumage traits of residents and challengers. *Behavioral Ecology and Sociobiology*, **60**, 663–671.
- Gustafsson, L., Qvarnström, A. & Sheldon, B. C. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature*, **375**, 311–313.
- Liebert, A. E., Gamboa, G. J., Stamp, N. E., Curtis, T. R., Monnet, K. M., Turillazzi, S. & Starks, P. T. 2006. Genetics, behavior and ecology of a paper wasp invasion: *Polistes dominulus* in North America. *Annales Zoologici Fennici*, **43**, 595–624.
- Maynard Smith, J. & Harper, D. G. C. 1988. The evolution of aggression: can selection generate variability? *Philosophical Transactions of the Royal Society B*, **319**, 557–570.
- Maynard Smith, J. & Harper, D. G. C. 2003. *Animal Signals*. Oxford: Oxford University Press.
- Parkash, R., Rajpurohit, S. & Ramniwas, S. 2008. Changes in body melanisation and desiccation resistance in highland vs. lowland populations of *D. melanogaster*. *Journal of Insect Physiology*, **54**, 1050–1056.
- Pärt, T. & Qvarnström, A. 1997. Badge size in collared flycatchers predicts outcome of male competition over territories. *Animal Behaviour*, **54**, 893–899.
- Price, T. D. 2006. Phenotypic plasticity, sexual selection and the evolution of colour patterns. *Journal of Experimental Biology*, **209**, 2368–2376.
- Qvarnström, A. 1997. Experimentally increased badge size increases male competition and reduces male parental care in the collared flycatcher. *Proceedings of the Royal Society B*, **264**, 1225–1231.
- Rohwer, S. 1975. The social significance of avian winter plumage variability. *Evolution*, **29**, 593–610.
- Rohwer, S. 1977. Status signaling in Harris sparrows: some experiments in deception. *Behaviour*, **61**, 107–129.
- Senar, J. C. 1999. Plumage coloration as a signal of social status. *Proceedings of the International Ornithological Congress*, **22**, 1669–1686.
- Senar, J. C. & Camerino, M. 1998. Status signalling and the ability to recognize dominants: an experiment with siskins (*Carduelis spinus*). *Proceedings of the Royal Society B*, **265**, 1515–1520.
- Shields, W. M. 1977. The social significance of avian winter plumage variability: a comment. *Evolution*, **31**, 905–907.
- Takahashi, M., Arita, H., Hiraiwa-Hasegawa, M. & Hasegawa, T. 2008. Peahens do not prefer peacocks with more elaborate trains. *Animal Behaviour*, **75**, 1209–1219.
- Tibbetts, E. A. 2008. Resource value and the context dependence of receiver behaviour. *Proceedings of the Royal Society B*, **275**, 2201–2206.
- Tibbetts, E. A. 2010. The condition dependence and heritability of signaling and nonsignal color traits in a paper wasp. *American Naturalist*, **175**, 495–503.
- Tibbetts, E. A. & Dale, J. 2004. A socially enforced signal of quality in a paper wasp. *Nature*, **432**, 218–222.
- Tibbetts, E. A. & Lindsay, R. 2008. Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. *Biology Letters*, **4**, 237–239.
- Tibbetts, E. A. & Shorter, J. R. 2009. How do fighting ability and nest value influence usurpation contests in *Polistes* wasps? *Behavioral Ecology and Sociobiology*, **63**, 1377–1385.
- Tibbetts, E. A., Mettler, A. & Levy, S. 2010. Mutual assessment via visual status signals in *Polistes dominulus* wasps. *Biology Letters*, **6**, 10–13.
- Usui, Y., Yamanaka, A., Fayezul Islam, A. T. M., Shahjahan, R. & Endo, K. 2004. Photoperiod- and temperature-dependent regulation of pupal beige/black polymorphism in the small copper butterfly, *Lycaena phlaeas daimio* Seitz. *Zoological Science*, **21**, 835–839.
- Whiting, M. J., Nagy, K. A. & Bateman, P. W. 2003. Evolution and maintenance of social status-signalling badges. In: *Lizard Social Behavior* (Ed. by S. F. Fox, K. McCoy & T. A. Baird), pp. 47–82. Baltimore, Maryland: Johns Hopkins University Press.
- Wilczynski, W. & Ryan, M. J. 1999. Geographic variation in animal communication systems. In: *Geographic Variation in Behaviour: Perspectives on Evolutionary Mechanisms* (Ed. by S. A. Foster & J. A. Endler), pp. 234–261. Oxford: Oxford University Press.
- Zanette, L. R. S. 2007. Group formation in a social wasp. Ph.D. thesis, University College London.
- Zanette, L. R. S. & Field, J. 2009. Cues, concessions and inheritance: dominance hierarchies in the paper wasp *Polistes dominulus*. *Behavioral Ecology*, **20**, 773–780.