

Selection for individual recognition and the evolution of polymorphic identity signals in *Polistes* paper wasps

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Abstract

Individual recognition (IR) requires individuals to uniquely identify their social partners based on phenotypic variation. Because IR is so specific, distinctive phenotypes that stand out from the crowd facilitate efficient recognition. Over time, the benefits of unique appearances are predicted to produce a correlation between IR and phenotypic variation. Here, we test whether there is an association between elevated phenotypic polymorphism and IR in paper wasps. Previous work has shown that *Polistes fuscatus* use variable colour patterns for IR. We test whether two less variable wasp species, *Polistes dominulus* and *Polistes metricus*, are capable of IR. As predicted, neither species is capable of IR, suggesting that highly variable colour patterns are confined to *Polistes* species with IR. This association suggests that elevated phenotypic variation in taxa with IR may be the result of selection for identity signals rather than neutral processes. Given that IR is widespread among social taxa, selection for identity signalling may be an underappreciated mechanism for the origin and maintenance of polymorphism.

Introduction

Phenotypic variation is essential for recognizing and differentiating between social partners. Recognition occurs when one individual, the receiver, discriminates between other individuals, the senders, using cues or signals produced by the senders (Sherman *et al.*, 1997; Mateo, 2004). There are many different types of recognition, including species, kin, nestmate and individual. Individual recognition (IR) is the most precise form of social recognition, because it requires receivers to uniquely identify each social partner (Beecher, 1989; Tibbetts & Dale, 2007).

Selection may act on the senders and/or the receivers during recognition system evolution. As a result, IR can evolve through two nonexclusive paths: (i) receiver cognition and perception may evolve so receivers can discriminate between individual conspecifics using neutral variation or (ii) the phenotypes of senders may evolve so that senders have distinctive, highly variable

features that permit easy individual identification (Johnstone, 1997; Dale *et al.*, 2001).

To date, most of the research on recognition systems has documented the extent of recognition, whereas less is known about the evolution of recognition systems and how selection has acted on sender phenotypes (Tibbetts & Dale, 2007). A method for testing whether recognition selects for the evolution of phenotypic variation is to assess the legacy of selection by comparing recognition abilities with the extent of phenotypic variation in a group of closely related species. If species with IR have more variable phenotypes than species lacking IR, the elevated phenotypic variation in taxa with IR may have evolved to facilitate accurate recognition. For example, swallow species with IR have more variable calls than species lacking IR, suggesting that selection has favoured call diversification in swallow species with IR (Beecher *et al.*, 1986; Medvin & Beecher, 1986; Medvin *et al.*, 1993).

Alternatively, selection may act on receiver cognition and perception alone, rather than the phenotypic variation in senders. For example, *Pachycondyla* spp. ants use distinctive chemical signatures for IR (D'Ettore & Heinze, 2005; Dreier *et al.*, 2007), although their

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chemical profiles are not more diverse than species that lack IR (Dreier & D'Etorre, 2009). Thus, IR may select for receivers that can differentiate between individuals based on otherwise neutral phenotypic variation. Selection for efficient IR systems can affect both sender and receiver phenotypes. Examining the associations between recognition abilities and phenotypic polymorphism can differentiate between these two processes.

Polistes paper wasps provide a good model for testing whether there is an association between the specificity of recognition and the extent of phenotypic variation within a species. The amount of phenotypic variation is dramatic across paper wasps (Enteman, 1904; Tibbetts, 2004). Some species such as *Polistes fuscatus* have extremely variable colour patterns, whereas other species such as *Polistes dominulus* and *Polistes metricus* have less variable colour patterns (Fig. 1). Less is known about *Polistes* recognition behaviour. In at least one species, *P. fuscatus*, the variable colour patterns are used for visual IR (Fig. 1, top row) (Tibbetts, 2002; Sheehan & Tibbetts, 2008), but *P. fuscatus* is the only wasp species where IR has been tested. Wasp species that appear to be less variable may be able to recognize individuals through two means. First, receiver perception may have evolved such that receivers can discriminate between individuals based on apparently minor colour variation. Second, wasps may use other sensory modalities, such as variable chemical signatures, to recognize individuals. As a result, it is important to test whether wasp species that lack variable visual features also lack IR abilities.

Here, we test the relationship between IR and phenotypic variation in three species of paper wasps (*P. fuscatus*, *P. dominulus* and *P. metricus*). First, we quantify the levels

of intraspecific colour pattern polymorphism in the species. Then, we experimentally test their ability to individually recognize conspecifics by comparing the response to familiar and unfamiliar individuals. If selection for IR in *Polistes* promotes and maintains highly variable colour patterns (Tibbetts, 2004), then species with low marking variability, such as *P. dominulus* and *P. metricus*, are not predicted to individually recognize conspecifics.

Methods

Colour pattern analysis

We describe the relative variation in colour patterns between species by assessing the distribution of colours on five different regions of the face (Fig. 2). Adobe Photoshop CS3 was used to measure the fraction of pixels in each of the five areas that were black, yellow or brown. These colour categories provide good estimates of the colour variability in *P. dominulus* and *P. metricus*. *Polistes fuscatus* have a wider range of brown colours, so any colour that was not black or yellow was classified as brown. This categorization underestimates the variability of *P. fuscatus*, so it provides a conservative method of scoring colouration with respect to our hypothesis. We collected wasps from nests at a number of sites in Michigan throughout the year. For colour analysis, 20 additional individuals from each species, all from different nests, were randomly chosen, freeze-killed and stored in a freezer at -20°C to ensure that colour patterns did not fade. All wasps were measured by a student with no knowledge of the specific experimental predictions.

Fig. 1 Portraits showing the colour pattern variation within each of the three species in this study. *Polistes fuscatus* (top row) have variable colouration in numerous regions of the face. Note that there is also a wide range of colour including numerous shades of brown. *Polistes dominulus* (middle row) has species-typical yellow markings on its face that show low levels of variability, although the black mark in the middle of the clypeus (the badge of status) is variable. *Polistes metricus* has some invariant colour regions (clypeus and inner eyes), but the species-typical markings on the frons and eyebrow show some variability in the extent of brown colouration. (See online publication at www.interscience.wiley.com for colour version of this figure.)



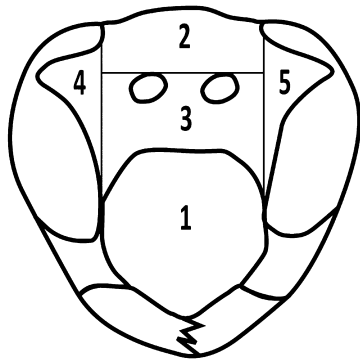


Fig. 2 Schematic of the regions of the wasp face considered in this study. (1) the clypeus, (2) the upper frons or 'eyebrow', (3) the frons, (4) the right inner eye and (5) the left inner eye. For the frons (region 3), the antennal sockets were not included in the total area.

Behavioural assessment of recognition abilities

We assessed the recognition abilities of *P. dominulus* and *P. metricus* by scoring the intensity of aggressive interactions between foundresses with and without prior social experiences with each other. Wasps of both species were collected near Ann Arbor, MI, in the early spring of 2008. We used 26 focal *P. dominulus* and 28 focal *P. metricus* foundresses in our trials. Immediately before the experiment, all individuals were housed individually and kept in social isolation. Previously, the *P. dominulus* foundresses had participated in choice experiments similar to those described elsewhere (Tibbetts, 2008; Tibbetts & Lindsay, 2008), in which they interacted with model wasps. We previously used methods similar to those described in the following paragraph to demonstrate that *P. fuscatus* can recognize individuals (Sheehan & Tibbetts, 2008), so we did not test this species again.

Our experimental design measured the abilities of both *P. dominulus* and *P. metricus* to remember individual social partners regardless of sensory modality. To ensure that foundresses had not encountered each other previously, all interactions were staged between foundresses collected from sites at least 2 km apart. In the first trial (day 0), two foundresses were introduced to each other in a small, sterile container and their interactions were filmed. After filming, they were housed together until the next day (day 1) at which point they were separated and returned to their initial solitary housing. One day later, the same two wasps were filmed interacting again (day 2). To ensure that any changes in aggression between days 0 and 2 were a result of IR and not of decreases in motivation over time, we paired the wasps with other unfamiliar social partners on the day before and after (days 1 and 3). On day 1, wasps were housed individually for approximately 5 h between separation

from their initial partner and meeting a new partner. If the wasps are able to recognize and remember social partners, they should be least aggressive when they interact with a known individual (day 2). Species capable of IR behave differently towards individuals with whom they share a history of prior interactions (Karavanich & Atema, 1998; D'Ettoire & Heinze, 2005; Dreier *et al.*, 2007; Sheehan & Tibbetts, 2008; Tibbetts *et al.*, 2008; Dreier & D'Ettoire, 2009). In this case, species with IR are predicted to be less aggressive towards the individual they have previously encountered (day 2) than towards individuals they are encountering for the first time (days 0, 1 and 3).

All of the behavioural trials lasted 2 h. Trials were videotaped and the first half hour of each trial was scored by an observer who was blind to the identity of wasps and the day the trial took place. Wasps engage in a range of aggressive and affiliative behaviours. Behaviours were rated on a scale of 0–4 with higher scores, indicating more intense aggression: (0) nonaggressive physical contact, (1) darts, (2) darting while snapping mandibles, (3) bites and (4) mounting or grappling. To compare the levels of aggression between trials, we calculated three measures: an intensity index, the number of nonaggressive interactions and an overall aggression index. The intensity index measured how intense aggressive interactions were and was calculated by summing the scores of aggressive interactions and dividing by the number of aggressive acts. The number of nonaggressive interactions was calculated by tallying the number of discreet nonaggressive interactions that took place. The overall aggression index took into account both aggressive and affiliative acts. The aggression index was calculated using the same method as the intensity index with the addition of the number of nonaggressive interactions in the denominator (Dreier *et al.*, 2007; Sheehan & Tibbetts, 2008). The indices and number of nonaggressive contacts were compared between days using Friedman's ANOVA and multiple comparisons (Sokal & Rohlf, 1995). *Post hoc* power tests were carried out using G*Power.

Results

Intraspecific colour pattern variation

Polistes fuscatus have far more variable colour patterns than either *P. dominulus* or *P. metricus*, and the differences in variation across species are obvious after examining a few pictures of each species (Fig. 1). The greater variability in the colour patterns of *P. fuscatus* arises from a combination of two factors. First, *P. fuscatus* have large amounts of variation in each area of the face (Fig. 3), whereas the variation in *P. dominulus* and *P. metricus* is limited to small areas of the face (clypeus in *P. dominulus* and antennal region in *P. metricus*). Second, there are more potential variants for each face region in *P. fuscatus*

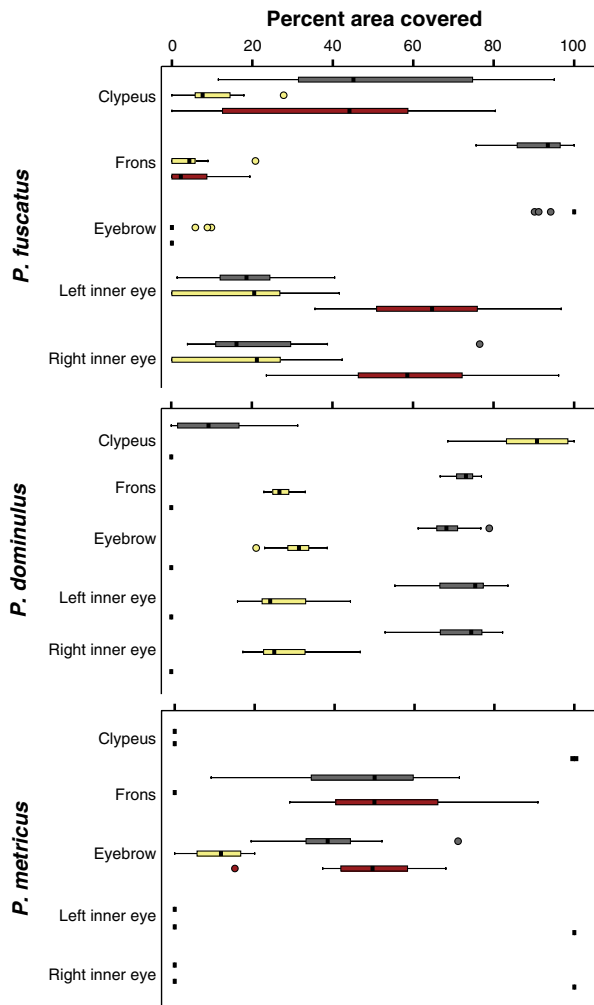


Fig. 3 *Polistes fuscatus* is by far the most variable of the three species. For each region, the percentage covered by each of the three colours is shown by the box plots. Black is at the top, yellow is in the middle and brown is at the bottom. Note that *P. fuscatus* shows variability in all of the regions and that the clypeus shows a wide of colouration patterns.

than *P. metricus* or *P. dominulus*. For example, the clypeus in *P. fuscatus* can contain a huge range of yellow, black and brown colour patterns (Fig. 1, top row). In contrast, the variation in *P. dominulus* is largely restricted to the size and shape of black clypeal spots, which previous research has shown acts as a signal of fighting ability (Tibbetts & Dale, 2004). Variation in *P. metricus* is restricted to the brown vs. black pigment in the eyebrow and frons areas. The variation in *P. metricus* is likely to be less visually apparent than the variation in *P. fuscatus* and *P. dominulus*, as the differences in colouration are quite subtle, and this area is typically obscured by the antennae during social interactions.

Behavioural recognition experiments

Polistes dominulus

There is no evidence of IR in *P. dominulus*. Aggressive encounters between wasps with prior histories of social interactions were just as intense as encounters between wasps that had not previously met (Fig. 4a. Friedman's ANOVA, $F_{(3, n=26)} = 1.51$, $P = 0.68$; *post hoc* power analysis, Power = 0.95). Additionally, the number of non-aggressive contacts did not differ between trials (Fig. 4b. Friedman's ANOVA, $F_{(3, n=26)} = 3.79$, $P = 0.29$; *post hoc* power analysis, Power = 1.00). Finally, the overall aggression index, which accounts for both aggressive and nonaggressive interactions, did not differ between trials (Fig. 4c. Friedman's ANOVA, $F_{(3, n=26)} = 5.67$, $P = 0.13$; *post hoc* power analysis, Power = 0.91).

Polistes metricus

There is no evidence of IR in *P. metricus*. The intensity of aggression declined after the first encounter in *P. metricus* (Fig. 5a. Friedman's ANOVA, $F_{(3, n=28)} = 18.06$, $P < 0.0001$; *post hoc* power analysis, Power = 0.95). However, there were no differences in the intensity of aggression after the first encounter. Aggressive intensity was similar among pairs of individuals with and without prior social histories (Fig. 5a). There were also a similar number of nonaggressive contacts across all trials (Fig. 5b. Friedman's ANOVA, $F_{(3, n=28)} = 1.72$, $P = 0.63$; *post hoc* power analysis, Power = 1.00). The overall aggression index, which incorporates both aggressive and nonaggressive interactions, was highest during the initial trial and lower in subsequent trials (Friedman's ANOVA, $F_{(3, n=28)} = 13.76$, $P = 0.003$; *post hoc* power analysis, Power = 0.95). Although aggression indices declined between a pair's first (day 0) and second (day 2) encounters [Nonparametric Tukey's HSD (Honestly significant difference), $P < 0.05$], there was no difference in aggression between the unfamiliar pairs on days 1 and 3 and the familiar pair on day 2 (Nonparametric Tukey's HSD, $P > 0.2$). In sum, there was no difference in the intensity of aggressive or nonaggressive interactions between wasp pairs that had interacted previously vs. pairs that lacked a prior history of social interactions.

Discussion

Paper wasp species differ markedly in their relative levels of intraspecific colour pattern variation. As predicted, the extent of colour variation is associated with recognition abilities in the three species tested. *Polistes fuscatus* are far more variable than *P. metricus* or *P. dominulus* and have robust long-term memories of individual conspecifics (Sheehan & Tibbetts, 2008). In contrast, *P. dominulus* and *P. metricus* have little variation in colour patterns. In both species, aggressive and affiliative behaviours did not vary with social history, indicating that neither species recognizes individual social partners.

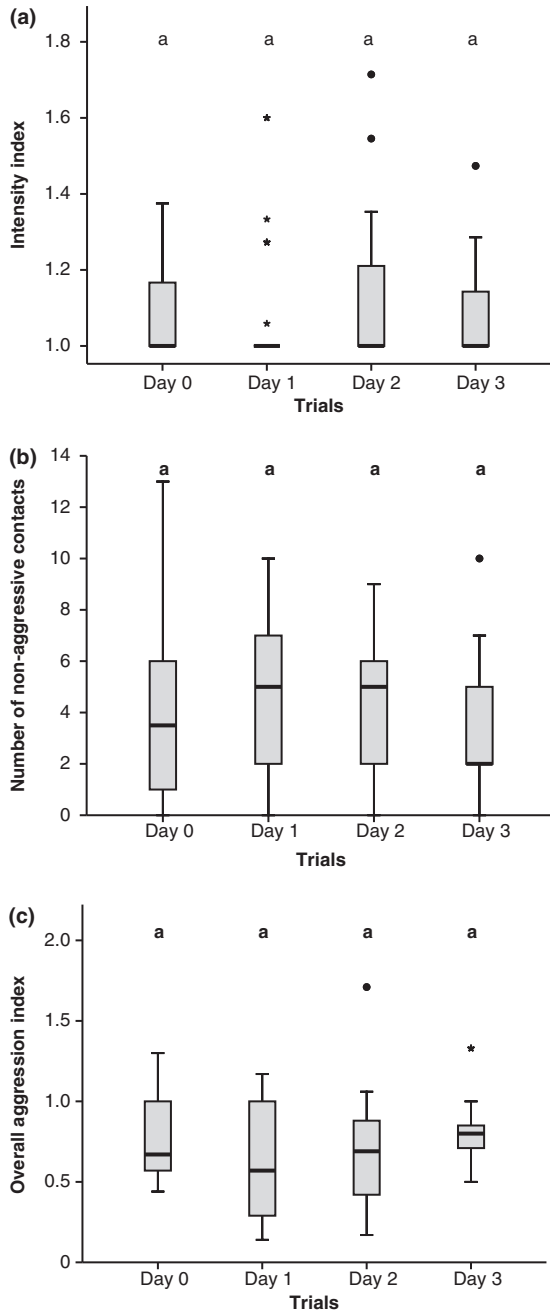


Fig. 4 *Polistes dominulus* show no evidence of individual recognition. Individuals with whom they have interacted previously (day 2) receive similar amounts of aggression as individuals they have never encountered (days 0, 1 and 3). The overall aggression indices (a), the number of nonaggressive contacts (b) and the intensity of aggressive acts (c) towards individual they have interacted with previously as individuals they have never encountered before does not differ. Days that are significantly different (Nonparametric Tukey's HSD, $P < 0.05$) are designated with different letters. Box plots show medians and quartiles.

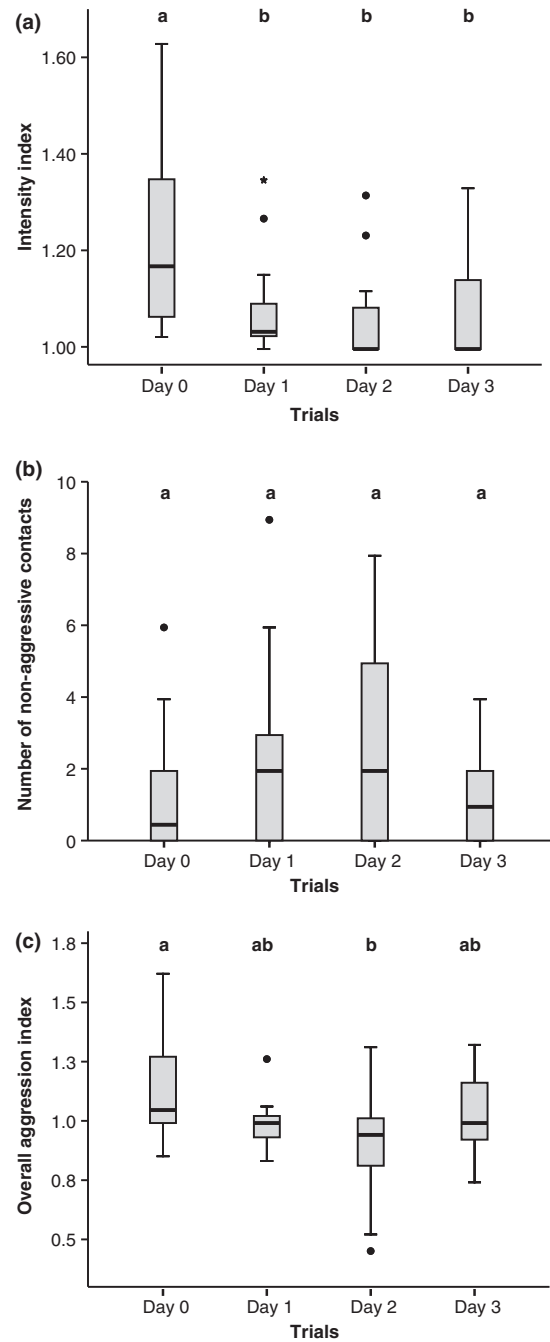


Fig. 5 Levels of aggression among *Polistes metricus* decline over time and do not show evidence of individual recognition. Interactions are the most aggressive during the first encounter and are less aggressive in subsequent encounters. When wasps re-encounter their social partner from days 0 to 2, they are less aggressive (a, c). However, they are similarly less aggressive to other new social partners on days 1 and 3, suggesting that motivation for aggression declines over time. Additionally, there are no differences in affiliative behaviours across trials (b). Days that are significantly different (Nonparametric Tukey's HSD, $P < 0.05$) are designated with different letters. Box plots show medians and quartiles.

The pattern of aggression across trials was slightly different in *P. metricus* than *P. dominulus*. *Polistes metricus* were more aggressive during their first encounter with a conspecific than during subsequent social encounters, whereas *P. dominulus* were similarly aggressive across all social encounters. The pattern of aggression in *P. metricus* is not evidence of IR, as aggression did not vary with individual social experience. Further, other species that lack IR show similar patterns of declining aggression over subsequent encounters (Dreier & D'Ettoire, 2009). Instead, the pattern of aggression may reflect differences in the social behaviour of the species. For example, *P. metricus* are less likely to form co-operative foundresses associations than *P. dominulus* or *P. fuscatus* and have extremely high rates of nest usurpation (Gamboa, 1978; Gamboa *et al.*, 2004). As a result, *P. metricus* may have a stronger initial aggressive response to conspecifics than *P. dominulus* or *P. fuscatus*.

The results of this study support a key prediction of the hypothesis that selection for efficient IR promotes and maintains phenotypic polymorphism. Selection for efficient social recognition has been hypothesized to favour the evolution of variable, distinctive phenotypes, thus promoting and maintaining polymorphism within populations (Dale *et al.*, 2001; Dale, 2006; Sheehan & Tibbetts, 2009). Over time, we expect selection for identity signalling to produce numerous phenotypes, such as those seen in *P. fuscatus* (Fig. 1, top row). In contrast, individuals in species lacking IR are not under selection to advertise their identity with unique phenotypes. Therefore, species without IR are predicted to have less variable phenotypes than those with IR, as we found in *Polistes*. A similar relationship between variation and recognition has been found in a few other species, suggesting that evolution can adaptively shape sender phenotypes to facilitate accurate recognition [e.g. comparative studies call variation in swallows (Beecher *et al.*, 1986; Medvin *et al.*, 1993) and penguins (Jouventin *et al.*, 1999; Jouventin & Aubin, 2002)].

An alternative hypothesis for the relationship between IR and phenotypic variation is that pre-existing variation is required to allow the evolution of IR. That is, pre-existing variation may be co-opted to allow IR rather than IR selecting for phenotypic variation. If pre-existing variation has been co-opted for recognition in the wasps, variation is predicted to be more strongly associated with a species' evolutionary history than its social behaviour. In fact, variable colour patterns in the *Polistes* are significantly associated with a species' social behaviour rather than its evolutionary history, suggesting that the benefits of social recognition have selected for phenotypic variation in certain taxa (Tibbetts, 2004). For example, *P. metricus* and *P. fuscatus* are sister species, yet foundresses of each species have different social behaviour and different patterns of phenotypic variation. Further, recent behavioural work has illustrated the mechanism that could drive the evolution of phenotypic

variation. Wasps with unique phenotypes receive less aggression during dominance contests than individuals with a common appearance, indicating that phenotypic variation provides benefits by facilitating recognition (Sheehan & Tibbetts, 2009). Although inferring the direction of evolutionary change can be difficult, current evidence suggests that IR selects for phenotypic variation rather than standing variation being co-opted for recognition behaviour in paper wasps. Future behavioural analysis on additional *Polistes* species with and without phenotypic variation will be important to confirm this pattern.

Data on chemical communication also suggest that IR has selected for variation rather than *vice versa*. In *Polistes*, variable cuticular hydrocarbon profiles have been found in all species examined to date (Gamboa, 2004). Both *P. dominulus* and *P. metricus* pay attention to the variation and use hydrocarbons to communicate nest membership (Singer & Espelie, 1996; Cini *et al.*, 2009) and individual fertility (Izzo *et al.*, in press). However, the results of this study demonstrate that neither *P. dominulus* nor *P. metricus* recognize individuals based on their variable hydrocarbon profiles. Therefore, pre-existing variation is not sufficient to allow the evolution of IR. Perhaps, the evolution of IR using chemical information is difficult in *Polistes*, because cuticular hydrocarbons already convey information about nestmate identity and fertility. Evolving a novel signal in a different modality may be easier than modifying chemical information to convey multiple, different kinds of information. Examining whether the presence of a pre-existing communication system constrains the evolution of other types of recognition within the same sensory modality presents an exciting possibility for future research. Overall, most evidence suggests that IR has been selected for variable visual features in *P. fuscatus*.

Mechanisms other than identity signalling may also maintain colour polymorphism in a population, including apostatic selection, mate choice for heterozygosity and alternative behavioural strategies. However, these alternatives are unlikely to explain the pattern of polymorphism in *P. fuscatus*. Apostatic selection favours phenotypic variation that is visually apparent to predators (Bond & Kamil, 2002). However, variation in *P. fuscatus* is primarily confined to the face (Tibbetts, 2002), which is useful during face-to-face social interactions but is not noticeable from a distance. Therefore, it is unlikely that variation in paper wasps has evolved to avoid detection by predators. Polymorphic colour patterns can also evolve via sexual selection when mates are chosen for novelty or mate heterozygosity (Farr, 1977; Eakley & Houde, 2004). This hypothesis predicts that the sex under strong sexual selection will be polymorphic. However, facial pattern polymorphism in *Polistes* is confined to females, even though males are lekking and experience strong sexual selection (Post & Jeanne, 1983; Matthessears & Alcock, 1986; Beani &

Turillazzi, 1988; Polak, 1993). Finally, phenotypic polymorphism is often associated with alternative social or mating strategies (Sinervo *et al.*, 2001; Svensson *et al.*, 2005). However, the colour pattern variation in *P. fuscatus* is not related to behavioural strategies such as founding strategy, dominance or social caste (Tibbetts, 2002). Therefore, although numerous mechanisms can maintain phenotypic polymorphism, most of these mechanisms are unlikely to be relevant to the variation in *Polistes* colour patterns. Instead, this study and other published work suggest that selection for identity signals is likely to have driven the evolution of the highly variable colour patterns in the paper wasps (Sheehan & Tibbetts, 2009).

Identity vs. quality signalling

The results of this study confirm that *P. fuscatus* and *P. dominulus* rely on different communication systems. *Polistes fuscatus* use IR (Tibbetts, 2002; Sheehan & Tibbetts, 2008), whereas *P. dominulus* are incapable of IR, relying instead on a visual signal of quality (Tibbetts, 2004; Tibbetts & Lindsay, 2008; Tibbetts *et al.*, in press). Despite the differences in communication behaviour, these species have very similar social systems. Both species display complex, flexible founding strategies, where queens may initiate a nest either alone or in co-operative groups. When multiple queens co-operate, they form a linear dominance hierarchy that influences work, reproduction and aggression (Roseler, 1991; Gamboa *et al.*, 2004). Foundress associations remain flexible for weeks, so foundresses of both species engage in aggressive contests with numerous familiar and unfamiliar individuals (West Eberhard, 1969; Reeve, 1991; Zanette & Field, 2009).

Given the similar social systems of *P. dominulus* and *P. fuscatus*, what accounts for the differences in the species' signalling systems? One possibility is that their social systems differ in subtle ways that have influenced signal evolution. Signals of fighting ability are expected to evolve when individuals compete with many unfamiliar rivals (Tibbetts & Safran, 2009), while identity signals are more important in smaller, stable groups (Tibbetts & Dale, 2007). Empirical data indicate that the quality signals in *P. dominulus* may be used primarily during interactions with non-nestmates (i.e. during early spring dominance contests before nesting groups are established or during attempted nest usurpation) (Tibbetts & Shorter, 2009; Zanette & Field, 2009). Identity signals in *P. fuscatus* are important during dominance interactions within established nests (Tibbetts, 2002). Therefore, identity and quality signals may reflect solutions to different types of social problems faced by *Polistes* wasps – non-nestmate interactions during colony foundation vs. linear dominance hierarchies among queens. Although communication researchers sometimes considers signal evolution to be a deterministic process,

with a set of social conditions leading to a certain type of signalling system, historical contingency may also play an important role in signal evolution.

Conclusions

IR requires receivers to distinguish between many individual social partners on the basis of unique cues (Tibbetts *et al.*, 2008). Recognition systems may evolve via two paths: (i) receivers may be favoured to pay attention to pre-existing phenotypic variation and (ii) senders may be favoured to advertise their identities with variable phenotypes. Distinguishing between these two non-mutually exclusive alternatives is challenging, although studies examining the relationship between phenotypic variation and recognition behaviour can provide insight into the dynamics of recognition system evolution. The results of this study demonstrate that two *Polistes* species without variable phenotypes lack IR, supporting the hypothesis that sender phenotypes have evolved to facilitate accurate recognition. Together with other published results (Tibbetts, 2004; Sheehan & Tibbetts, 2009), the current study provides evidence that the variable colour patterns in *P. fuscatus* have evolved via selection for easily recognizable identity signals rather than neutral processes.

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References

- Beani, L. & Turillazzi, S. 1988. Alternative mating tactics in males of *Polistes dominulus* (Hymenoptera, Vespidae). *Behav. Ecol. Sociobiol.* **22**: 257–264.
- Beecher, M.D. 1989. Singaling systems for individual recognition – an information-theory approach. *Anim. Behav.* **38**: 248–261.
- Beecher, M.D., Medvin, M.B., Stoddard, P.K. & Loesche, P. 1986. Acoustic adaptations for parent-offspring recognition in swallows. *Exp. Biol.* **45**: 179–193.
- Bond, A.B. & Kamil, A.C. 2002. Visual predators select for crypticity and polymorphism in virtual prey. *Nature* **415**: 609–613.
- Cini, A., Gioli, L. & Cervo, R. 2009. A quantitative threshold for nest-mate recognition in a paper social wasp. *Biol. Lett.* **5**: 459–461.
- D'Ettore, P. & Heinze, J. 2005. Individual recognition in ant queens. *Curr. Biol.* **15**: 2170–2174.
- Dale, J. 2006. Intraspecific variation in coloration. In: *Bird Coloration, Volume 2, Function and Evolution* (G.E. Hill & K.J. McGraw, eds), pp. 36–86. Harvard University Press, Cambridge, MA.

- Dale, J., Lank, D.B. & Reeve, H.K. 2001. Signaling individual identity versus quality: a model and case studies with ruffs, queleas, and house finches. *Am. Nat.* **158**: 75–86.
- Dreier, S. & D'Etorre, P. 2009. Social context predicts recognition systems in ant queens. *J. Evol. Biol.* **22**: 644–649.
- Dreier, S., van Zweden, J.S. & D'Etorre, P. 2007. Long-term memory of individual identity in ant queens. *Biol. Lett.* **3**: 459–462.
- Eakley, A.L. & Houde, A.E. 2004. Possible role of female discrimination against 'redundant' males in the evolution of colour pattern polymorphism in guppies. *Proc. R. Soc. Lond. B Biol. Sci.* **271**: S299–S301.
- Enteman, W. 1904. *Coloration in Polistes*. Carnegie Institute of Washington, Washington, DC.
- Farr, J.A. 1977. Male rarity or novelty, female choice behavior, and sexual selection in the guppy, *Poecilia reticulata* Peters (Pisces: poeciliidae). *Evolution* **31**: 162–168.
- Gamboa, G.J. 1978. Intraspecific defense – advantage of social cooperation among paper wasp foundresses. *Science* **199**: 1463–1465.
- Gamboa, G.J. 2004. Kin recognition in eusocial wasps. *Ann. Zool. Fenn.* **41**: 789–808.
- Gamboa, G.J., Noble, M.A., Thom, M.C., Togal, J.L., Srinivasan, R. & Murphy, B.D. 2004. The comparative biology of two sympatric paper wasps in Michigan, the native *Polistes fuscatus* and the invasive *Polistes dominulus* (Hymenoptera, Vespidae). *Insect. Soc.* **51**: 153–157.
- Izzo, A., Wells, M., Huang, Z. & Tibbetts, E.A. Cuticular hydrocarbons correlate with fertility, not dominance in a paper wasp, *Polistes dominulus*. *Behav. Ecol. Sociobiol.* in press.
- Johnstone, R.A. 1997. Recognition and the evolution of distinctive signatures: when does it pay to reveal identity? *Proc. R. Soc. Lond. B Biol. Sci.* **264**: 1547–1553.
- Jouventin, P. & Aubin, T. 2002. Acoustic systems are adapted to breeding ecologies: individual recognition in nesting penguins. *Anim. Behav.* **64**: 747–757.
- Jouventin, P., Aubin, T. & Lengagne, T. 1999. Finding a parent in a king penguin colony: the acoustic system of individual recognition. *Anim. Behav.* **57**: 1175–1183.
- Karavanich, C. & Atema, J. 1998. Individual recognition and memory in lobster dominance. *Anim. Behav.* **56**: 1553–1560.
- Mateo, J.M. 2004. Recognition systems and biological organization: the perception component of social recognition. *Ann. Zool. Fenn.* **41**: 729–745.
- Matthessears, W. & Alcock, J. 1986. Hilltopping behavior of *Polistes commanchus-navajoe* (Hymenoptera, Vespidae). *Ethology* **71**: 42–53.
- Medvin, M.B. & Beecher, M.D. 1986. Parent offspring recognition in the barn swallow (*Hirundo rustica*). *Anim. Behav.* **34**: 1627–1639.
- Medvin, M.B., Stoddard, P.K. & Beecher, M.D. 1993. Signals for parent offspring recognition: a comparative-analysis of the begging calls of cliff swallows and barn swallows. *Anim. Behav.* **45**: 841–850.
- Polak, M. 1993. Competition of landmark territories among male *Polistes canadensis* (L) (Hymenoptera, Vespidae): large-size advantage and alternative mate-acquisition tactics. *Behav. Ecol.* **4**: 325–331.
- Post, D.C. & Jeanne, R.L. 1983. Male reproductive behavior of the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *Z. Tierpsychol. – J. Comp. Ethol.* **62**: 157–171.
- Reeve, H.K. 1991. *Polistes*. In: *The Social Biology of Wasps* (K.G. Ross & R.W. Matthews, eds), pp. 99–148. Comstock, Ithaca.
- Roseler, P. 1991. Reproductive competition during colony establishment. In: *The Social Biology of Wasps* (K. Ross & R. Matthews, eds), pp. 309–335. Cornell University Press, Ithaca, NY.
- Sheehan, M.J. & Tibbetts, E.A. 2008. Robust long-term social memories in a paper wasp. *Curr. Biol.* **18**: R851–R852.
- Sheehan, M.J. & Tibbetts, E.A. 2009. Evolution of identity signals: frequency-dependent benefits of distinctive phenotypes used for individual recognition. *Evolution* **63**: 3106–3113.
- Sherman, P.W., Reeve, H.K. & Pfennig, D.W. 1997. Recognition systems. In: *Behavioural Ecology: An Evolutionary Approach* (J.R. Krebs & N.B. Davies, eds), pp. 69–96. Blackwell Science Ltd, Oxford.
- Sinervo, B., Bleay, C. & Adamopoulou, C. 2001. Social causes of correlational selection and the resolution of a heritable throat color polymorphism in a lizard. *Evolution* **55**: 2040–2052.
- Singer, T.L. & Espelie, K.E. 1996. Nest surface hydrocarbons facilitate nestmate recognition for the social wasp, *Polistes metricus* Say (Hymenoptera: Vespidae). *J. Insect Behav.* **9**: 857–870.
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry*, 3rd edn. W.H. Freeman and Company, New York.
- Svensson, E.I., Abbott, J. & Hardling, R. 2005. Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. *Am. Nat.* **165**: 567–576.
- Tibbetts, E.A. 2002. Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proc. R. Soc. Lond. B Biol. Sci.* **269**: 1423–1428.
- Tibbetts, E.A. 2004. Complex social behaviour can select for variability in visual features: a case study in *Polistes* wasps. *Proc. R. Soc. Lond. B Biol. Sci.* **271**: 1955–1960.
- Tibbetts, E.A. 2008. Resource value and the context dependence of receiver behaviour. *Proc. R. Soc. Lond. B Biol. Sci.* **275**: 2201–2206.
- Tibbetts, E.A. & Dale, J. 2004. A socially enforced signal of quality in a paper wasp. *Nature* **432**: 218–222.
- Tibbetts, E.A. & Dale, J. 2007. Individual recognition: it is good to be different. *Trends Ecol. Evol.* **22**: 529–537.
- Tibbetts, E.A. & Lindsay, R. 2008. Visual signals of status and rival assessment in *Polistes dominulus* paper wasps. *Biol. Lett.* **4**: 237–239.
- Tibbetts, E.A. & Safran, R. 2009. Co-evolution of plumage characteristics and winter sociality in new and old world sparrows. *J. Evol. Biol.* **22**: 2376–2386.
- Tibbetts, E.A. & Shorter, J.R. 2009. How do fighting ability and nest value influence usurpation contests in *Polistes* wasps? *Behav. Ecol. Sociobiol.* **63**: 1377–1385.
- Tibbetts, E.A., Sheehan, M.J. & Dale, J. 2008. A testable definition of individual recognition. *Trends Ecol. Evol.* **23**: 356.
- Tibbetts, E.A., Mettler, A. & Levy, S. Mutual assessment via visual status signals in *Polistes dominulus* wasps. *Biol. Lett.*, doi:10.1098/rsbl.2009.0420.
- West Eberhard, M.J. 1969. *The Social Biology of Polistine Wasps*. Museum of Zoology, University of Michigan, Ann Arbor.
- Zanette, L. & Field, J. 2009. Cues, concessions, and inheritance: dominance hierarchies in the paper wasp *Polistes dominulus*. *Behav. Ecol.* **20**: 773–780.

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