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Complex social behaviour can select for variability in visual features: a case study in *Polistes* wasps

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The ability to recognize individuals is common in animals; however, we know little about why the phenotypic variability necessary for individual recognition has evolved in some animals but not others. One possibility is that natural selection favours variability in some social contexts but not in others. *Polistes fuscatus* wasps have variable facial and abdominal markings used for individual recognition within their complex societies. Here, I explore whether social behaviour can select for variability by examining the relationship between social behaviour and variability in visual features (marking variability) across social wasp taxa. Analysis using a concentrated changes test demonstrates that marking variability is significantly associated with nesting strategy. Species *with* flexible nest-founding strategies have highly variable markings, whereas species *without* flexible nest-founding strategies have low marking variability. These results suggest that: (i) individual recognition may be widespread in the social wasps, and (ii) natural selection may play a role in the origin and maintenance of the variable distinctive markings. Theoretical and empirical evidence suggests that species with flexible nesting strategies have reproductive transactions, a type of complex social behaviour predicted to require individual recognition. Therefore, the reproductive transactions of flexible species may select for highly variable individuals who are easy to identify as individuals. Further, selection for distinctiveness may provide an alternative explanation for the evolution of phenotypic diversity.

Keywords: individual recognition; skew theory; ornamentation; dominance hierarchies

1. INTRODUCTION

The phenotypic diversity within a single species can be remarkable, from the polymorphic underwings of *Catocala* moths (Kamil & Bond 2001), to the white and blue colour phases of the lesser snow goose (Cooke *et al.* 1995), to the markedly different sizes and shapes of leaf-cutting ants (Hölldobler & Roces 2001). Many different selection pressures are thought to cause the phenotypic diversity within species, ranging from sexual selection to frequency-dependent selection. Benefits derived from being individually distinctive and easily recognizable may offer an important, but largely neglected, explanation for the origin and maintenance of phenotypic diversity (Beecher 1989; Johnstone 1997; Dale *et al.* 2001).

Individual recognition occurs in many different modalities, including olfactory, visual and acoustic (reviewed in Dale *et al.* 2001). In every modality, the trait used for recognition must be highly variable to allow accurate discrimination of individuals (Dale *et al.* 2001). There are two possible explanations for the evolution of the phenotypic variability necessary for individual recognition: (i) no selection favouring distinctiveness: the variability could be neutral or functional in a non-recognition context and have been co-opted for recognizing conspecifics; and (ii) selection favouring distinctiveness: the variability could benefit individuals by making them readily recognizable and this benefit may have driven the evolution of phenotypic variability. One way to differentiate between these alternatives is to test whether social behaviour predicted to involve individual recognition is associated with frequent gains and/or infrequent losses of variability. This type of association supports the hypothesis that variability has evolved because distinctiveness benefits individuals of species with this social behaviour.

Theoretical work suggests that several types of complex social behaviour could select for the kind of variable markings necessary for individual recognition, including territoriality (Ydenberg *et al.* 1988), reciprocal altruism (Crowley *et al.* 1996), monogamous pairing (Dale *et al.* 2001), dominance (Barnard & Burk 1979; Van Rhijn & Vodegel 1980; Dawkins & Guilford 1991) and reproductive transactions (when group members yield reproduction to each other in exchange for benefits in a manner predicted by transactional models). Examining the relationship between variability and social behaviour will also provide valuable insight into which behaviours actually select for distinctive, recognizable individuals, as little empirical research has addressed this topic (Beecher 1989).

Social wasps in the genus *Polistes* are an attractive taxon in which to examine whether social behaviour can select for distinctiveness. First, it is known that individual recognition occurs in at least one species in this genus. In *Polistes fuscatus*, wasps use variation in facial and abdominal markings to recognize their nest-mates as individuals (Tibbetts 2002). Second, experimental results suggest that the social behaviour of *P. fuscatus* may favour wasps with variable distinctive markings; easily recognizable wasps receive less aggression from their nest-mates than unrecognizable wasps (Tibbetts 2002). Third, *Polistes* is a large genus and one finds diverse social behaviours of varying complexity among its many species. Although specific information on social behaviour is available for only a few *Polistes* species,

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models and empirical data indicate that nest-founding strategy is a useful proxy for social behaviour (Reeve & Keller 2001), and nest-founding strategies are well documented. Species have one of three nest-founding strategies: multiple foundress (all nests are started by multiple foundresses) single foundress (all nests are started by a single foundress), or flexible (nests can be started by a single foundress or by multiple foundresses). All *Polistes* species have workers for much of the colony cycle. Workers and queens have identical marking variability (Tibbetts 2002), as workers are fertile and may become queens (Reeve *et al.* 1998). Here, I test for a relationship between nest-founding strategy and marking variability across the *Polistes*.

(i) If variable markings are associated with all nesting strategies, no conclusion can be drawn, but the pattern suggests that worker interactions may be sufficient to select for variability.
(ii) If there is no association between variable markings and nesting strategies, nesting strategy may not be a useful proxy for social behaviour or social behaviour may not have selected for variability in the *Polistes*.
(iii) A significant association between nesting strategy and variable markings (a) suggests a role for natural selection in the origin and maintenance of variable, distinctive markings, and (b) provides insight into the type of social behaviour that may select for distinctiveness.

2. METHODS

(a) *Variability data*

Information on the marking variability of each species was collected by examining specimens from the *Polistes* collections at the Museum of Natural History in New York, and Cornell University in Ithaca, NY. All variability data were collected blind with respect to species and social behaviour. Therefore, I was able to assess the repeatability of variability scores by independently scoring the variability of seven species in each museum. Variability was scored only when at least 10 specimens of a species were available (the mean number of specimens examined was 58; range 10–200). I collected data on facial and abdominal variability, as both are used for individual recognition in *P. fuscatus* (Tibbetts 2002). The number of marking variants in a species was determined by counting the number of facial or abdominal areas that varied and the number of different marking variants for each of these areas. Across the species examined, I found five discrete facial areas that varied: inner eye, outer eye, clypeus edge, middle clypeus and 'eyebrow' (the area dorsal to the antennae; figure 1). There were nine discrete abdominal areas that varied: the middle of each abdominal segment (1–5) and the edge of abdominal segments 1–4. I calculated the number of possible combinations of variable areas and variants to get each species' total variability. For example, in figure 1, there are three areas that vary and two variants for each of these areas. Therefore, this species has $2^3 = 8$ total variants. This method of assessing a species' variability assumes that marking areas vary independently of each other, an appropriate assumption given the distribution of markings in *P. fuscatus* (Tibbetts 2002). Further, this method of scoring a species's variability provides an estimate of the maximum variability of each species rather than the exact number of variants in each species. Species with less than five variants on either face or abdomen were categorized as low variability species. All species with five or more variants in either face or abdomen were termed high variability species. I chose five variants as the cut-off point between low and high variability species as I was looking for the exceptional variability expected in a species selected for distinctiveness; accurate discrimination of individuals requires that all individuals on a nest have different markings. This cut-off point was determined after gathering all variability data, but was blind with respect to the variability of particular species and their social behaviour. Most low variability species had one variant and the most high variability species had eight or more variants, so the results are not sensitive to the specific cut-off point. If eight variants were used as the cut-off, the mean probability of the observed association between variability and social behaviour occurring by random chance is 0.010. If three variants were used as the cut-off, the mean probability is 0.066. Therefore, any cut-off between three and eight yields similar results.

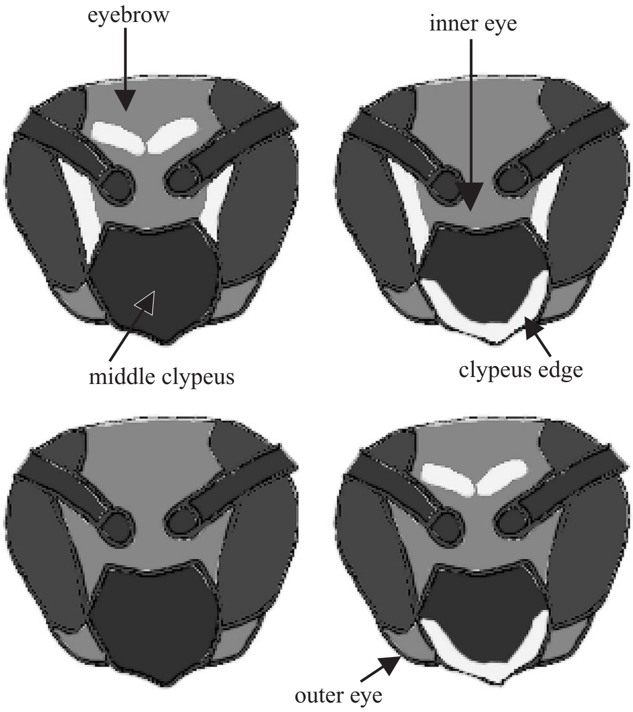

Figure 1. Illustration of four different wasp faces. The five general facial areas that vary across wasp taxa are labelled.

Variability data were collected on 69 species of *Polistes*; 14 species of *Mischocyttarus*, the genus most closely related to *Polistes* (Carpenter 1996), were also examined to provide an outgroup.

(b) *Behavioural data*

Searching the literature yielded data on nest-founding strategies of 25 *Polistes* species. I defined multiple-foundress species as those in which more than 98% of nests were started by multiple foundresses, and single-foundress species as those in which more than 98% of nests were started by a single foundress. Species with intermediate rates of singly and multiply founded nests were categorized as having 'flexible' nest-founding strategies.

(c) *Phylogenetic analysis*

Carpenter's (1996) taxon-area phylogeny was used for the analysis. His tree is based on a consensus tree that used 33 morphological characters and species group distributions. Behavioural data on 25 *Polistes* species and variability data on 69 *Polistes* species plus an outgroup were mapped onto the tree using MCCLADE (Maddison & Maddison 1992). The hypothesis that

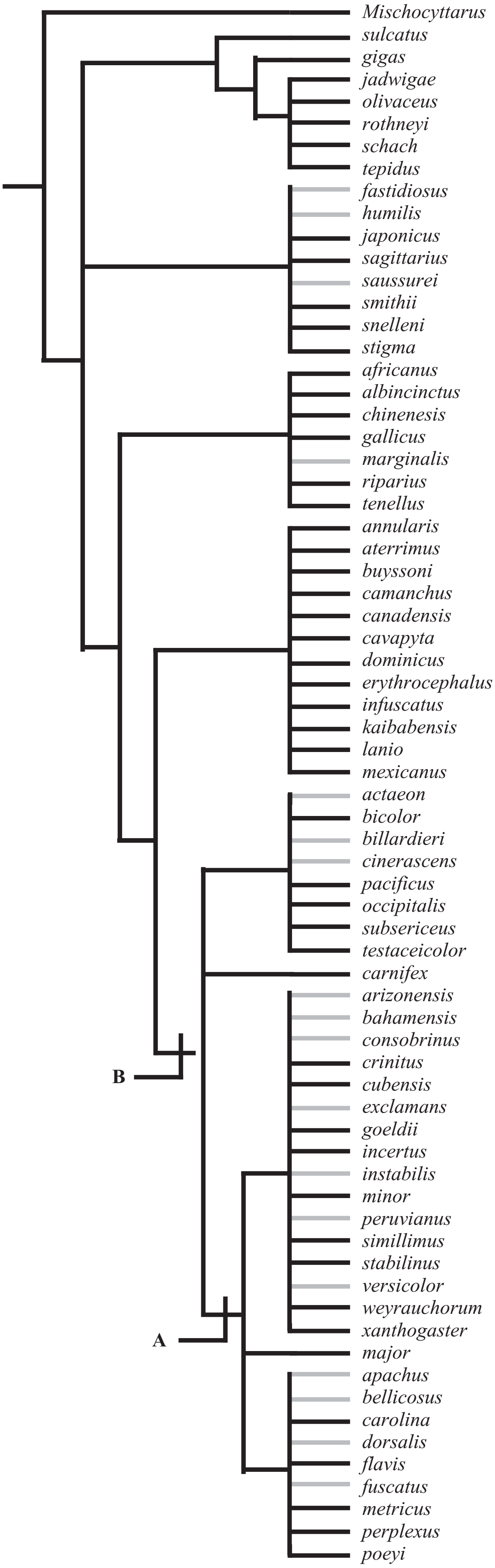

Figure 2. The distribution of marking variability among 69 *Polistes* species using Carpenter's (1996) phylogeny. Black indicates low variability. Grey indicates high variability. The most parsimonious reconstruction of variability is shown. Analysis was also performed using less parsimonious reconstructions of variability (marked with A and B) to ensure the results are robust.

changes in marking variability (dependent variable) are associated with nest-founding strategy (independent variable) was tested using Maddison's (1990) concentrated changes test. This test examines whether changes in marking variability occur more frequently on branches where species have the predicted nest-founding strategy or an unknown nest-founding strategy than expected by chance. The null hypothesis is that gains and losses of variable markings are equally probable on every branch. Specifically, the test addresses whether a flexible nesting strategy facilitates the evolution of variability (if gains of variability are associated with flexible nesting strategies) and/or the maintenance of variability (losses of variability are not associated with flexible nesting strategy). The number of gains and losses of variability was estimated by McClade, using the most parsimonious reconstruction of character evolution (figure 2). The concentrated changes test is sensitive to the number of gains and losses, so the data were also analysed with the most conservative numbers of gains and losses to ensure that the results were robust. Carpenter's (1996) phylogeny contains polytomies. As the concentrated changes test cannot be performed with polytomies, all polytomies were randomly resolved by McClade. Then the concentrated changes test was run for each of five randomly selected resolutions. The exact probability of the observed relationship occurring by chance was calculated by McClade in most analyses. In two cases, exact values could not be calculated, so probabilities were estimated with a 1000-iteration simulation.

(d) *Correlation analysis*

The relationship between marking variability and nesting strategy was also analysed independently of phylogeny by using a χ^2 analysis.

3. RESULTS

There was no relationship between the number of specimens examined and the classification of a species with respect to marking variability (high or low) ($p = 0.32$, $t = 1$, d.f. $= 47$). Therefore, the number of specimens examined did not bias the variability categorizations.

Specimens of seven species were examined in both museums to determine the repeatability of variability categorizations. Three species were categorized as highly variable in both museums, and four species were categorized as low variability in both museums (Fisher's exact test: $p = 0.028$). Therefore, each sample was an accurate representation of that species' true variability and my method of scoring variability yielded consistent results, even between museums.

The distribution of marking variability in 69 species of *Polistes* is shown in figure 2. The ancestral state is low variability. Highly variable markings evolved a minimum of five times. The distribution of marking variability and nest-founding strategy in 25 *Polistes* species is shown in figure 3. All eight species with highly variable markings have a flexible nesting strategy, but there are four species with a

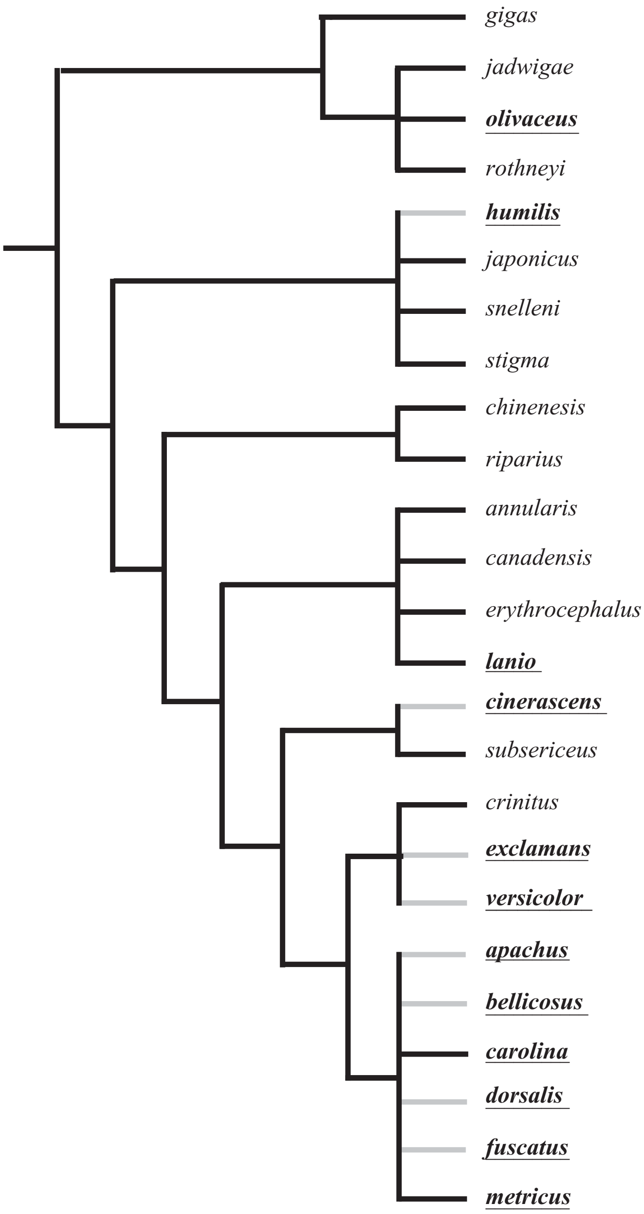

Figure 3. The distribution of marking variability and nest-founding strategy in 25 *Polistes* species. Black indicates low variability. Grey indicates high variability. Underlined species have flexible nest-founding strategies. Other species are multiple foundress or single foundress.

flexible nesting strategy that do not have highly variable markings (*P. olivaceous*, *P. lanio*, *P. metricus* and *P. carolina*).

Table 1 gives the probabilities that the observed association between changes in variability and nest-founding strategy would occur through random chance. (Probabilities are given for three reconstructions of ancestral states and five random resolutions of the polytomies seen in figure 3.) The probability of the observed association occurring through random chance is below 0.05 for every analysis.

Similar results are found when the relationship between nest-founding strategy and variability is analysed using a χ^2 analysis. There are 13 species with non-variable markings and non-flexible nesting strategies, eight species with variable markings and flexible nesting strategies, four species with non-variable markings and flexible nesting strategies, and zero species with variable markings and a non-flexible nesting strategy. This distribution is significantly different from random ($\chi^2 = 12.7$, $p = 0.0004$). If the non-flexible species are more specifically categorized into single-foundress and multiple-foundress species, the statistical difference between nesting strategy and variability is also significantly different from random ($\chi^2 = 12.7$, $p = 0.0017$; 10 non-variable single-foundress species, three non-variable multiple-foundress species, zero variable single-foundress species, and zero variable multiple-foundress species). Therefore, flexibly nesting species are significantly more likely to have variable markings, regardless of whether one controls for phylogeny.

4. DISCUSSION

There are eight *Polistes* species with the kind of highly variable markings necessary for individual recognition, suggesting that individual recognition is widespread in the *Polistes*. Further, gains of marking variability are significantly clustered in areas of the phylogeny where species have an unknown or flexible nest-founding strategy (foundresses have the option of starting a nest alone or in a group). In areas of the phylogeny where foundresses always nest alone or always nest in a group, all species have invariant markings. There is also a significant association between nesting strategy and marking variability independent of phylogenetic relationships; flexible species have variable markings and non-flexible species have non-variable markings.

The robust association between marking variability and flexible nesting strategies suggests that variable markings have evolved because some aspect of flexible nest-founding selects for distinctive individuals. The complex social behaviour of flexible species is the most plausible selection pressure, as markings are known to be a social signal, unobtrusive without close interaction, and not associated with physiological or behavioural differences (Tibbetts 2002). Further, *P. fuscatus* who are easily recognizable received less aggression from their nest-mates than *P. fuscatus* who are unrecognizable, suggesting that being recognizable may provide social benefits (Tibbetts 2002). Finally, theory and empirical results indicate that flexible species (such as *P. fuscatus*) have reproductive transactions (reviewed in Reeve & Keller 2001), precisely the type of complex social behaviour predicted to favour distinctiveness (Beecher 1989; Johnstone 1997; Dale *et al.* 2001).

Distinctiveness probably provides individual and colony-level benefits in species with reproductive transactions. At the individual level, distinctive wasps probably receive less aggression than non-distinctive wasps. Theoretical and empirical evidence indicates that, in flexible species, the dominant foundress concedes a fraction of the group's reproduction to the subordinate in exchange for the subordinate's help (reproductive transactions (Reeve & Ratnieks 1993; Reeve *et al.* 2000; Reeve & Keller 2001)). The dominant makes such concessions because each subordinate has the option of starting her own nest (Reeve 2000). Precise reproductive shares vary with rank, so it is not surprising that there is constant aggression between wasps of adjacent ranks. Wasps of other ranks receive little aggression, probably because they are not perceived as an

Table 1. Results of the concentrated changes test for marking variability (dependent character) and nest-founding strategy (independent character).
(Each number is the probability of the observed association between changes in variability and nest-founding strategy given the null model, in which gains and losses of variability are randomly distributed on the phylogeny. Probabilities are given for three reconstructions of ancestral states and five random resolutions of the polytomies seen in figure 3.)

	tree 1	tree 2	tree 3	tree 4	tree 5	mean across trees
most parsimonious reconstruction	0.003	0.003	0.002	0.008	0.005	0.004
variability gained at A	0.012	0.013	0.012	0.038	0.042	0.023
variability gained at B	0.011	0.010	0.011	0.050	0.038	0.024

immediate threat (Downing & Jeanne 1985). A wasp who clearly advertises her identity (and rank) with distinctive markings should receive aggression from only those adjacent in the dominance hierarchy, whereas a non-distinctive wasp should receive aggression from nest-mates of all ranks as they continually assess her dominance. Indeed, unrecognizable *P. fuscatus* received more aggression than recognizable *P. fuscatus* (Tibbetts 2002). At the colony level, individual recognition should greatly reduce intra-colony conflict, thereby increasing colony productivity. In flexible species, rank determines the amount of reproduction, food and aggression that wasps receive and from whom they receive them (Röseler 1991). Shares of reproduction and food are carefully monitored and cheaters are punished (Reeve & Nonacs 1993; Tibbetts & Reeve 2000). Without individual recognition, these complex behaviours could be very costly to coordinate; but they would be relatively stable and cheap if individuals were distinctive. Therefore, distinctiveness probably provides individual and colony benefits in flexible species, thereby selecting for easily recognizable wasps with highly variable markings.

The absence of variability in single-foundress and multiple-foundress species suggests that interactions among multiple foundresses and workers are not sufficient to select for variable markings, probably because these species lack the carefully monitored and contested reproductive shares of flexible species. In multiple-foundress species, the dominant foundress can monopolize colony reproduction, as subordinates do not have good alternative nesting options; a subordinate's probability of successfully usurping or founding another nest is extremely low (reviewed in Reeve 1991). Worker rank also does not determine daily shares of reproduction (Reeve 1991). Without complex reproductive partitioning, these species probably experience less selection for variable recognizable markings. Future research on the precise social behaviour of every *Polistes* species will be useful to increase our knowledge of reproductive transactions, as they are a controversial topic (Seppä *et al.* 2002). However, these comparative results add to the compelling body of evidence that reproductive transactions are confined to *Polistes* with flexible nesting strategies (reviewed in Reeve & Keller 2001).

There are four species that are exceptions to the relationship between nest-founding strategy and variability: *P. olivaceous*, *P. lanio*, *P. metricus* and *P. carolina* have flexible nest-founding strategies but low variability markings. Why do they not have highly variable markings? Either (i) the social behaviour of these species does not favour distinctive markings, or (ii) distinctive markings are favoured, but the necessary variation has not arisen. Although nest-founding strategy is a useful proxy for social behaviour, the correlation between transactions and flexible nesting may be imperfect. For example, *P. carolina* is the only flexible species thought to lack transactions (Field *et al.* 1998; Seppä *et al.* 2002; but see Reeve & Keller 2001), so *P. carolina*'s lack of marking variability lends further support to the hypothesis that transactions select for distinctive individuals. Distinctive markings are also unnecessary if multiple-foundress associations are rarely larger than two foundresses. Data on the specific number of associating foundresses in each species are not available, but it would be interesting to test whether the exceptions rarely nest in associations larger than two foundresses. Further, my categorizations of nest-founding strategies are conservative. Species were categorized as 'flexible' if more than 2% of nests were multiply founded after averaging multiple founding rates across all locations. For example, *P. metricus*, a species without variable markings, is single-foundress near Houston (Hughes *et al.* 1993) but has a flexible nest-founding strategy in Kansas (Gamboa 1978). Do *P. metricus* in Kansas have more variable markings than *P. metricus* in Texas? Alternatively, the exceptions may have social behaviour that selects for variable distinctive markings, but the marking variation has not arisen. This explanation is plausible as *P. olivaceous* and *P. lanio*, both non-variable species with flexible nesting strategies, are not closely related to species with variable markings or flexible nesting strategies. To date, there is not enough information on these species to be certain why these species are exceptions. Nevertheless, across the whole group, highly variable markings are overwhelmingly associated with flexible strategies.

The strong association between marking variability and nest-founding strategy in *Polistes* suggests that (i) individual recognition is common in *Polistes* species with flexible nesting strategies, and (ii) marking variability evolved because wasps with flexible nesting strategies benefit by being easy to recognize. The benefits probably involve reduced aggression within transactional dominance hierarchies and increased stability of reproductive transactions. Selection for distinctiveness may offer another general explanation for the evolution of phenotypic diversity. Many creatures with complex social behaviours have been noted for their unusually variable features (e.g. humans, wolves and wild dogs). Perhaps social dynamics have selected for distinctive variable markings in these taxa as well.

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