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Visual signals of individual identity in the wasp *Polistes fuscatus*

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Individual recognition is an essential component of interactions in many social systems, but insects are often thought incapable of the sophistication necessary to recognize individuals. If this were true, it would impose limits on the societies that insects could form. For example, queens and workers of the paper wasp *Polistes fuscatus* form a linear dominance hierarchy that determines how food, work and reproduction are divided within the colony. Such a stable hierarchy would be facilitated if individuals of different ranks have some degree of recognition. *P. fuscatus* wasps have, to our knowledge, previously undocumented variability in their yellow facial and abdominal markings that are intriguing candidates for signals of individual identity. Here, I describe these highly variable markings and experimentally test whether *P. fuscatus* queens and workers use these markings to identify individual nest-mates visually. I demonstrate that individuals whose yellow markings are experimentally altered with paint receive more aggression than control wasps who are painted in a way that does not alter their markings. Further, aggression declines towards wasps with experimentally altered markings as these novel markings become familiar to their nest-mates. This evidence for individual recognition in *P. fuscatus* indicates that interactions between insects may be even more complex than previously anticipated.

Keywords: individual recognition; insect vision; social behaviour; dominance hierarchies; pattern recognition

1. INTRODUCTION

Individual recognition is important in the social lives of many organisms, including birds, mammals, reptiles and fishes. Social behaviour that involves individual recognition in these vertebrate taxa, such as territoriality, dominance hierarchies, monogamous pairing and lekking mating systems (Dale *et al.* 2001), also occurs in insects (Choe & Crespi 1997). These social systems could not function without some degree of individual recognition, but insects are often thought to be incapable of individually identifying conspecifics (Anderson & McShea 2001).

Polistes paper wasps are a group of insects with the type of complex yet stable interactions that should require individual recognition. Many *Polistes fuscatus* colonies are founded by multiple queens (foundresses) in early spring. During colony foundation, foundresses on the same nest (co-foundresses) are extremely aggressive as they fight to establish relative dominance rank (West-Eberhard 1969). Within a few days, the intensity and number of aggressive acts decreases dramatically and co-foundresses establish a stable, linear dominance hierarchy. As workers emerge, they also integrate into this dominance hierarchy (Reeve 1991). An individual wasp's position in the hierarchy influences most of her behaviour, including her share of the colony's reproduction (Reeve 1991), food (Röseler 1991) and work (West-Eberhard 1969), as well as the amount of aggression she receives (Downing & Jeanne 1985). Wasps respond to nest-mates according to their rank, but they do not fight to establish relative rank every time they meet. So how do wasps assess the specific ranks of their nest-mates?

The most dominant *P. dominulus* queen develops a characteristic chemical signature at worker emergence that may allow nest-mates to recognize her as the most dominant female (Sledge *et al.* 2001). However, only the most dominant female has a distinct signature, so it is unclear how stability is maintained in the precise linear dominance hierarchy involving all colony members. Furthermore, foundresses' chemical signatures are indistinguishable early in the colony cycle (Sledge *et al.* 2001), so foundresses must use another mechanism to identify rank during that period. Thus, *P. fuscatus* wasps behave as if they can recognize individual nest-mates (Downing & Jeanne 1985), but there has been no satisfactory answer for how this recognition occurs. One possibility is that individuals differ coarsely in rank-related phenotypes such as glandular secretions, but another is that group members are sufficiently distinctive that individuals, not merely ranks, can be discriminated.

P. fuscatus wasps have obvious and highly variable facial and abdominal markings, which are intriguing candidates for signals of individual identity. However, there are four other hypotheses for what these markings may signal: (i) no signal value; (ii) nest membership; (iii) quality; or (iv) intra-nest relatedness (see table 1). I describe the remarkably variable facial and abdominal markings of *P. fuscatus* wasps. Then, I demonstrate that the markings are not correlated with wasp body condition, which indicates that the markings are unlikely to be signals of quality. Finally, I present results from three independent sets of experiments in which I experimentally altered the markings of focal wasps with paint. The results conform exactly to predictions of the individual recognition hypothesis, while they do not support predictions of the four other hypotheses. Evidently, foundresses and workers of the paper wasp *P. fuscatus* use the variation in their nest-mates' facial and abdominal markings to visually recognize their nest-mates as individuals.

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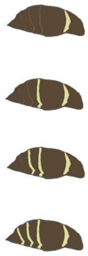

9	3	13	12	11	13	3	2	5	2	1	4
11	1	13	16	4	8	4	3	9	3	2	8
6	2	8	5	5	14	5	2	8	2	1	3
3	1	3	4	3	6	7	1	7	2	0	1

Figure 1. The relative frequency of marking combinations in a population of 259 *Polistes fuscatus* from 38 nests in Ithaca, New York. Top row: facial marking categories. Left column: abdominal marking categories. Outer eye markings were excluded to keep the table to a manageable size.

Figure 2. Portraits of four *Polistes fuscatus* collected from Ithaca, New York.

2. METHODS

(a) *Descriptive studies*

Unmarked foundresses and workers were removed from their nest with forceps during the early morning. In total, 259 wasps from 38 nests were examined. Each wasp's markings were examined, then characterized using the following categories: inner eye stripe (present or absent), eyebrows (diagonal yellow stripes dorsal to the antennae) (present or absent), outer eye stripe (present or absent), clypeus pattern (all dark, yellow tip or yellow edging) and yellow abdominal stripes (on segments 1, 1–2, 1–3 or 1–4) (figures 1 and 2). These categorizations do not capture these wasps' full variability, but they do provide a simple way of grouping the different types of markings to analyse the relationship between markings and condition. Most foundresses ($n = 40$) were weighed to 2 mg precision after characterizing their markings. Subsequently, all wasps were labelled with enamel paint and returned to their nests. For analyses of the relationship between markings and quality, I later determined the rank of 42 foundresses from 19 of these nests using behavioural observations of stereotyped dominance interactions (West-Eberhard 1969).

(b) *Experimental studies*

The basic protocol involved experimental treatments in which the markings of focal wasps were altered with paint, and control treatments in which focal wasps were painted without altering their markings. Nest-mate responses to focal wasps were then recorded and compared between experimental and control treatments. *P. fuscatus* nests used in these experiments were located on the eaves of houses and barns in Ithaca, New York, USA. All wasps were labelled on the thorax with enamel paint for easy identification at least one day before the recognition experiments. The focal wasp was taken from her nest with forceps between 05.00 and 07.00, when wasps are cool and inactive. After collection, each focal wasp was painted (described below) and placed in a container for 2–4 h to allow the paint to dry and her nest to warm. All experiments involved paired experimental and control treatments in which the same wasp was used for both treatments. To control for order effects, half of the experimental treatments were performed before the controls. In these cases, the focal wasp's yellow markings looked the same during both treatments, because the paint from the experimental alteration was still on the focal wasp during the control. Although markings did not vary between experimental and control trials, nest-mate familiarity with experimentally altered markings did vary. The latter means that differences in the amount of aggression received by focal wasps were caused by nest-mate familiarity with the markings, not by the specific markings that were changed in the experimental treatment. This experimental design is critical to differentiate between individual recognition and the other potential hypotheses for the signal value of *P. fuscatus* markings. Treatments were usually performed on consecutive days (a day was missed in three cases due to bad weather) and the order of the treatments was randomized. After focal wasps were returned to their nest, all aggressive acts towards them were recorded (i.e. dart, lunge, mount and bite; for a detailed description of these aggressive behaviours, see West-Eberhard (1969)). Aggression levels were normalized by taking the $\log_{10}$ of the number of aggressive acts. Results were analysed with two-tailed paired *t*-tests, unless otherwise noted.

(i) *Facial markings*

Foundresses

Experiments to test whether foundresses use facial markings to recognize the individual identity of their nest-mates were conducted late in the preworker phase of colony development, between 10 and 27 June 2001. Tests were conducted on 11 individuals from 11 multiple-foundress colonies. For the experimental treatment, one or two bilateral pairs of facial markings were changed, either by obscuring yellow markings with black paint ($n = 8$) or by adding yellow markings with yellow paint ($n = 3$). For the control, a similarly sized black area of the wasp's

Table 1. Predictions of the five alternative hypotheses for the signal value of *Polistes fuscatus* markings. (+, relationship predicted; −, no relationship predicted; ?, no clear prediction.)

prediction	neutral	nest-mate recognition	quality	intra-colony kin recognition	individual recognition	observed
aggression towards focal experimental wasp decreases over time	−	?	−	−	+	+
focal experimental wasp is chased off nest	−	+	−	−	−	−
markings are correlated with condition	−	−	+	−	−	−

face was painted with black paint. Four general facial areas were painted (inner eye, outer eye, eyebrow, clypeus). The specific area painted in experimental and control treatments varied from wasp to wasp. However, across all treatments, every facial area was painted on at least some wasps. In some cases, painting a specific area with black paint altered a wasp's appearance (because of a yellow mark in that area), while in other cases it did not (because there was no yellow mark in that area). For example, if a wasp had a yellow inner eye stripe, painting her inner eye with black paint would alter her appearance (experimental treatment). However, if a wasp did not have a yellow inner eye stripe, painting the inner eye with black paint would not alter her appearance (control treatment). This design allowed a demonstration of the fact that experimental responses were caused by *alteration* of facial markings, not by covering specific facial areas with paint. After painting, the focal wasp was returned to her nest between 09.00 and 10.30 and the nest was videotaped for 120 min to determine whether aggression towards the experimentally altered wasp declined over time.

Workers

Experiments to test facial recognition in workers were conducted during the worker phase of colony development, between 8 July and 14 August 2000 on 12 individuals from 12 colonies. This experiment was performed in the same manner as the foundress experiment described above, but nests were only videotaped for 30 min after the focal wasp was returned to the nest. In these experiments, five wasp faces were altered with black paint and seven wasp faces were altered with yellow paint.

(ii) *Abdominal markings*

To determine whether abdominal stripes are also involved in individual recognition, a similar set of experiments in which the abdominal markings of workers were altered was performed from 9 to 28 July 2001. Twelve individuals from 10 colonies were used. In the experimental treatment, abdominal markings were altered by covering one or two yellow stripes with black paint ($n = 7$) or by adding a stripe with yellow paint ($n = 5$). In the control, a similarly sized black area on the abdomen was painted with black paint. In this experiment, focal wasps were released near their nest and allowed to return to the nest naturally, instead of being placed on their nest. After each wasp returned to her nest, the nest was videotaped for 30 min.

3. RESULTS

(a) *Descriptive study*

There is a striking degree of variability in the presence or absence of facial and abdominal markings of *P. fuscatus* (figures 1 and 2) and further variation in the width and length of all yellow markings: from small dots to long, bold stripes (not indicated in the figures). Some wasps had other markings such as middle clypeus blotches, yellow abdominal dots, upper clypeus stripes or combinations of clypeus edge and tip coloration. Also, some wasps had abdominal, outer eye and clypeus patterns in brown and black. I did not experimentally test whether brown markings were meaningful for recognition, so I do not discuss them further. However, these brown markings are an additional source of variability that could be useful for individual recognition.

The yellow markings are not correlated with any measure of foundress condition, so they are unlikely to be a signal of dominance or quality. There was no significant relationship between foundress founding strategy (single versus multiple-foundress nest) and any markings (χ^2 $p = 0.27$–0.90, five comparisons, $n = 87$ wasps). There was also no significant relationship between any marking and the foundress's rank (χ^2 $p = 0.09$–0.61, five comparisons, $n = 42$ wasps) or weight (*t*-test $p = 0.39$–0.92, five comparisons, $n = 40$ wasps). Furthermore, there was no relationship between the total number of yellow markings on a foundress and her founding strategy ($p = 0.74$, d.f. $= 86$, $t = 0.33$), rank ($p = 0.5$, d.f. $= 41$, $t = 0.68$), or weight (regression $p = 0.7$, $n = 40$, $r = 0.06$).

(b) *Recognition experiments*

(i) *Facial individual recognition experiments*

On average, a focal foundress received significantly more aggression in the half hour after yellow facial markings were added or obscured in the experimental treatment than in the half hour after paint was applied but no yellow markings were added or obscured in the control treatment (figure 3*a*; $p = 0.02$, d.f. $= 10$, $t = 3.14$). Aggression towards focal experimental wasps declined over time; they received much more aggression in the half hour immediately after they were returned to their nests than in the half hour beginning 90 min after their return ($p = 0.004$, d.f. $= 9$, $t = 3.8$). However, the amount of aggression that focal control wasps received did not change over the 2 h ($p = 0.85$, d.f. $= 9$, $t = -0.19$). These results indicate that nest-mates were aggressive towards a wasp whose yellow facial markings were altered because she had become unfamiliar, not because her altered markings signalled something different about her (e.g. less related, lower quality). Although experimentally altered wasps received significantly more aggression than control wasps immediately after they were returned to their nest, there was no difference in the amount of aggression that experimental and control wasps received one and a half hours later ($p = 0.55$, d.f. $= 9$, $t = 0.6$). Therefore, the new

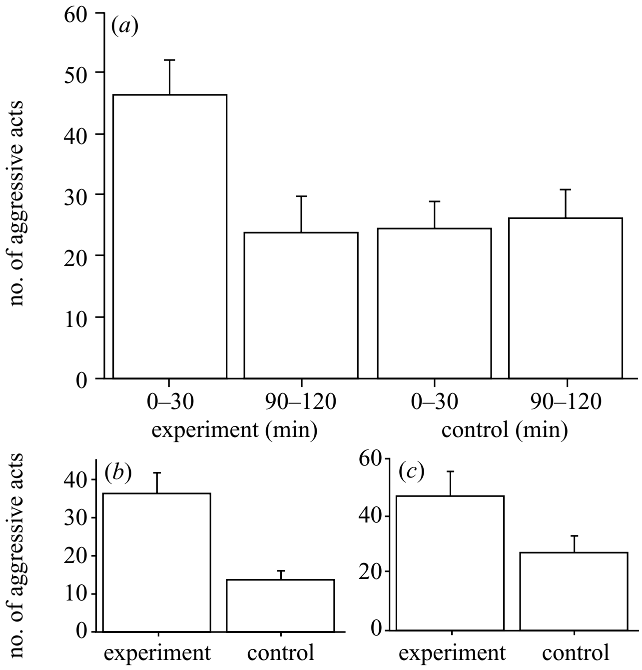

Figure 3. Mean (+ s.e.) number of aggressive acts directed towards focal wasps during a half-hour period. Experimental and control periods began immediately after the focal wasps were returned to their nests. Experimental periods involved alteration of (*a*) foundress facial markings (including aggression data from 90 min after focal wasp introduction), (*b*) worker facial markings, and (*c*) worker abdominal markings.

yellow markings of the experimentally altered wasps may have been learned by their nest-mates within 2 h.

Focal workers also received significantly more aggression after their yellow facial markings were altered in the experimental treatment than after their face was painted without altering yellow facial markings in the control (figure 3*b*; $p = 0.0014$, d.f. = 11, $t = 4.22$). In seven cases, the experimental treatment was performed before the control, so the focal workers' yellow markings looked the same during both trials. The only difference between experimental and control treatments in these seven cases was the novelty of the altered wasps' appearance. Aggression significantly declined between experimental and control treatments in these seven cases ($p = 0.018$, d.f. = 6, $t = 3.2$), indicating that the novelty of the experimental wasps' appearance, not some specific feature of their new appearance, induced aggression.

In the two experiments described above, four facial areas were painted to alter the yellow facial markings of the focal wasp: inner eye, outer eye, clypeus and eyebrow. To test whether higher aggression depended on the specific facial area painted, I pooled results from the foundress and worker facial recognition experiments. Then, I split the entire sample of 23 pairs according to whether or not each of the four facial areas was altered in the experimental treatment. Each *p*-value in table 2 is the result of a one-tailed paired *t*-test test comparing the amount of aggression that the focal wasp received after experimental and control treatments. There is a significant difference between experimental and control treatments in every category, regardless of whether or not a specific area was painted. Therefore, the experimental effects were not caused by altering one specific facial area. Furthermore, all four facial areas were used for recognition.

After pooling the worker and foundress data, I also tested whether the experimental effect differed between cases in which yellow markings were obscured with black paint and cases in which yellow markings were added with yellow paint. Both experimental treatments are significantly different from controls (yellow marks obscured $p = 0.0006$, d.f. = 14, $t = 4.18$; yellow marks added $p = 0.018$, d.f. = 7, $t = 3.06$).

(ii) *Abdominal individual recognition experiment*

Focal workers received significantly more aggression after the number of abdominal stripes was experimentally altered than after the control treatment in which the abdomen was painted without altering the stripes' appearance (figure 3*c*; $p = 0.034$, d.f. = 11, $t = 2.43$). In seven trials, the experimental treatment was performed before the control treatment, so the focal wasps' yellow markings looked the same during both periods. Aggression significantly declined between experimental and control treatment in these seven cases (one-tailed *t*-test $p = 0.03$, d.f. = 6, $t = 2.37$), so the unfamiliarity of the experimental wasp's abdominal markings induced aggression, while her specific abdominal-stripe pattern did not.

4. DISCUSSION

These experiments indicate that wasps initially respond with aggression towards nest-mates whose yellow facial or abdominal markings have been altered. These results indicate that the pattern of facial and abdominal markings of *P. fuscatus* is used for individually recognizing nest-mates (table 1) and these results fail to support the four other hypotheses for the signal value of these markings: (i) no signal value, (ii) nest membership, (iii) quality and (iv) intra-nest relatedness.

(i) Focal wasps received more aggression after their yellow markings were altered than after they were painted without altering the appearance of their yellow markings. This indicates that the yellow markings have some signal value.

(ii) Wasps use chemical cues on the cuticle to identify their nest-mates (Gamboa 1996) and wasps perceived as non-nest-mates are mauled and chased off the nest within 5 min (Bura & Gamboa 1994). After reintroduction to their nest, no focal wasp was mauled and all focal wasps remained on the nest for more than 5 min. Thus, all wasps were accepted as nest-mates after marking alteration, indicating that the markings are not used for nest-mate recognition.

(iii) If a wasp's markings signal something about her quality or condition, there should be some relationship between markings and founding strategy, weight or dominance rank. There are no such relationships, indicating that these markings do not signal anything about quality or condition.

(iii, iv) Finally, the quality and intra-colony kin recognition hypotheses predict that the amount of aggression that a wasp receives should remain

Table 2. Focal wasps received significantly more aggression in experimental than control treatments, regardless of which facial area was painted in the experimental treatment.

changed in experimental treatment?	inner eye	outer eye	clypeus	eyebrow
yes	$p = 0.003$ $n = 8$	$p = 0.015$ $n = 7$	$p = 0.008$ $n = 12$	$p = 0.04$ $n = 7$
no	$p = 0.001$ $n = 15$	$p = 0.0003$ $n = 16$	$p < 0.0001$ $n = 11$	$p = 0.0001$ $n = 16$

constant as long as she looks the same. Thus, a wasp with altered yellow markings might receive more aggression if she is perceived differently (i.e. as of lower quality or less related), but the amount of aggression she receives should remain constant as long as her markings are constant. I found that aggression towards wasps with experimentally altered markings significantly declined during the 2 h observation period, indicating that the unfamiliarity of a wasp's new markings, not something else about the new markings (new indication of status, relatedness, etc.) caused the aggression. Also, in half of the trials for each experiment, the experimental treatment was performed before the control, so the focal wasp's yellow markings looked the same during the two sampling periods. However, the focal wasp still received more aggression during the experimental than control period. These results provide still more evidence that aggression towards the focal wasp was induced by the novelty of her appearance, not by her specific markings. Therefore, the experimental results do not support key predictions of the neutral, nest-mate recognition, quality and intra-colony kin recognition hypotheses.

However, the experimental results conform exactly to predictions of the individual recognition hypothesis. Under this hypothesis, an altered wasp with unrecognized markings should receive more aggression from her nest-mates as they attempt to assess her dominance and place her in the hierarchy. The aggression received by the unrecognized wasp should be the type of mild aggression associated with intra-colony competition (darts, lunges, mounts). After a period of testing, aggression towards the unrecognized wasp should decrease as nest-mates learn her rank and markings. In the experiments, wasps with an experimentally altered appearance received a great deal of mild aggression. Also, aggression towards experimentally altered wasps declined over time, as nest-mates learned the new markings and ranks of the focal wasps. These results accord with findings that aggression between newly associating foundresses rapidly declines after their first meeting (Röseler 1991). All these results demonstrate that *P. fuscatus* wasps use facial and abdominal markings to recognize their nest-mates as individuals.

(a) *Visual acuity in wasps*

The use of visual cues for individual recognition in *P. fuscatus* is somewhat surprising, as insects are often thought to have relatively poor form vision. However, compound eyes have excellent spatial resolution over short distances (Land 1997) and signals of individual identity are probably only used within nests. Although no one knows exactly how well *Polistes* wasps see, they probably have a minimum interommatidial angle of one degree, like honeybees and *Vespa vulgaris* wasps (Land 1997). In Ithaca, the average worker phase nest is about 5 cm in diameter. Those two values can be used to estimate that *P. fuscatus* wasps might be able to resolve visual points that are 0.87 mm apart, from anywhere on the nest. Facial markings are from 0.25–0.50 mm in width and 1–2 mm in length, but abdominal markings are longer and interactions occur at close distances. Therefore, current data are consistent with the conclusion that *P. fuscatus* eyes are sufficiently acute to detect variability in facial and abdominal markings. It will be interesting to test the acuity of *Polistes* eyes directly to improve these estimates. Further, *Polistes* may have specific adaptations, like pattern recognition templates (Heisenberg 1995), for discerning the markings of their nest-mates.

(b) *Signalling individual identity*

The present, experimental results show that wasps use variation in facial and abdominal markings to identify individual nest-mates, an ability that probably provides substantial benefits. For example, learning the identities and relative ranks of nest-mates would enable wasps to respond appropriately to nest-mates: submissively to dominant individuals and aggressively to potentially threatening individuals just below them in the dominance hierarchy. Thus, there are clear benefits to recognition behaviour, providing a potential explanation for why wasps can recognize the individual identities of their nest-mates.

However, in order for the variable markings in wasps to be specially evolved signals of individual identity, it is essential that individual wasps experience inclusive fitness benefits through being individually recognizable (Dale *et al.* 2001). One potential benefit of recognizability in *P. fuscatus* may be reduced aggression from nest-mates. Wasps are most aggressive towards individuals flanking them in the dominance hierarchy (Downing & Jeanne 1985). A distinctive wasp who clearly advertises her identity and rank would receive most aggression from wasps adjacent in the dominance hierarchy. A non-distinctive wasp whose rank is unclear could be perceived as a threat by nest-mates of all ranks. Consequently, signalling her identity could vastly reduce the amount of aggression that a wasp receives.

One other context in which both recognition and recognizability could benefit co-nesting *P. fuscatus* females is in the partitioning of reproduction. There is good evidence that subordinate *Polistes* foundresses are given a fraction of a colony's reproduction in exchange for staying and helping to rear offspring on that colony (Reeve *et al.* 2000). Foundresses seem to keep track of exactly how much reproduction each foundress receives and aggressively punish cheating (Reeve & Nonacs 1992). Foundresses may also use similar rules to regulate food sharing in a colony (Tibbetts & Reeve 2000). It is difficult to imagine how foundresses could keep track of individual shares of food and reproduction without the ability to recognize individual nest-mates.

5. CONCLUSION

P. fuscatus wasps have extremely variable cuticular markings on the face and abdomen that are described here for the first time, to my knowledge. *Polistes fuscatus* use these markings to visually identify foundress and worker nestmates as individuals.

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REFERENCES

Anderson, C. & McShea, D. W. 2001 Individual versus social complexity, with particular reference to ant colonies. *Biol. Rev.* **76**, 211–237.

Bura, E. A. & Gamboa, G. J. 1994 Kin recognition by social wasps: asymmetric tolerance between aunts and nieces. *Anim. Behav.* **47**, 977–979.

Choe, J. C. & Crespi, B. J. 1997 *The evolution of social behavior in insects and arachnids*. New York: Cambridge University Press.

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.

Downing, H. A. & Jeanne, R. L. 1985 Communication of status in the social wasp *P. fuscatus* (Hymenoptera, Vespidae). *Z. Tierpsychol.* **67**, 78–96.

Gamboa, G. J. 1996 Kin recognition in social wasps. In *Natural history and evolution of paper wasps* (ed. S. Turillazzi & M. J. West-Eberhard), pp. 161–177. New York: Oxford University Press.

Heisenberg, M. 1995 Pattern recognition in insects. *Curr. Opin. Neurobiol.* **5**, 475–481.

Land, M. F. 1997 Visual acuity in insects. *A. Rev. Entomol.* **42**, 147–177.

Reeve, H. K. 1991 Polistes. In *The social biology of wasps* (ed. K. G. Ross & R. W. Matthews), pp. 99–148. Ithaca, NY: Comstock Publishing Associates.

Reeve, H. K. & Nonacs, P. 1992 Social contracts in wasp societies. *Nature* **359**, 823–825.

Reeve, H. K., Starks, P. T., Peters, J. M. & Nonacs, P. 2000 Genetic support for the evolutionary theory of reproductive transactions in social wasps. *Proc. R. Soc. Lond.* B **267**, 75–79. (DOI 10.1098/rspb.2000.0969.)

Röseler, P. F. 1991 Reproductive competition during colony establishment. In *The social biology of wasps* (ed. K. G. Ross & R. W. Matthews), pp. 309–335. Ithaca, NY: Comstock Publishing Associates.

Sledge, M. F., Boscaro, F. & Turillazzi, S. 2001 Cuticular hydrocarbons and reproductive status in the social wasp *Polistes dominulus*. *Behav. Ecol. Sociobiol.* **49**, 401–409.

Tibbetts, E. A. & Reeve, H. K. 2000 Aggression and resource sharing among foundresses in the social wasp *Polistes dominulus*: testing transactional theories of conflict. *Behav. Ecol. Sociobiol.* **48**, 344–352.

West-Eberhard, M. J. 1969 The social biology of polistine wasps. *Misc. Publ. Mus. Zool. Univ. Michigan* **140**, 1–101.