

hypothesis has been equivocal in other systems, but now appears clear in *P. dominulus*. Losers were more likely to suffer continuing aggression from the dominant female if they had a more broken (higher-rank) pattern.

Going beyond correlation, Tibbetts and Dale manipulated the clypeus spots with yellow and black paint. To one member of a pair that had not previously interacted, the authors either added a spot, obliterated an existing spot, or added paint in ways that did not change the existing pattern. After these females had established a clear dominance relationship, dominant females continued to be aggressive towards subordinates whose painted marks indicated an increase in status. The result clearly supports the hypothesis that there are social costs to erroneously high status signals: cheating subordinates are punished.

The study had several puzzling features, however. The key result discussed above relates to behaviour after dominance had been established. Surprisingly, though, manipulating the spot pattern had no effect on behaviour before rank was established. Also, females painted with high-status marks were no more likely to attain dominant status than were those painted with low-status marks, or controls. If extra marks give a badge of high status, then their owner should be more likely to become dominant.

Another curiosity is that after dominance was established, the dominant females were also more aggressive towards subordinates painted to look even more subordinate. This is hard to explain in a two-female system. But wasps often begin nests in groups of more than two. A female with marks indicating very low rank that acted instead like a second-ranked female could plausibly be perceived by the dominant female as a threat and receive more aggression. A further unpredicted result is that unpainted subordinates were aggressive towards painted dominants, whether they were painted with a higher- or a lower-status mark than that of their 'true' status. In ten cases, the unpainted subordinate female even overthrew the painted dominant; these cases were evenly divided between those in which the dominant was painted with a higher- or a lower-status mark.

Also interesting is that the correlation of spot number or brokenness with head width is very weak, accounting for only 7% or 3% of the variance, respectively. A reliable cue of condition should account for more of the variance. Perhaps head width is not the best measure of condition, and perhaps the clypeus marks are actually correlated with a better, as-yet-unknown measure. But the marks are fixed in the pupal stage, and are not altered by later feeding and overwintering, which are known to affect condition. It seems that if clypeus marks are status badges, they are not conventional ones.



Figure 1 **Badge of status.** *Polistes dominulus* wasps show variation in the number and brokenness of spots on the clypeus, above the mouth. Tibbetts and Dale¹ find that these measures provide an indicator of how dominant or subordinate an individual is; dishonesty brings social costs.

Tibbetts and Dale were careful to control for numerous factors that might have influenced the outcome of the contests. First, they paired wasps for mass. Second, they paired individuals that were unrelated and came from sites kilometres apart, so they could not have had any prior interactions. (In this species, females begin nests with relatives or nearby non-relatives with whom they are likely to have previously interacted².) A further reason why the paired individuals could not have benefited from recognizing each other is that they were videotaped immediately after pairing. However, it is possible that they normally use individual recognition as well as status badges, as individual recognition can occur, at least in another *Polistes* species⁴.

It might seem remarkable that wasps have such sophisticated abilities. But social competition is a very strong selective force¹⁰. Pinyon jays can infer rank by watching others interact¹¹. Viruses can cheat¹². Perhaps it should be no surprise that social wasps can recognize individuals and their rank. ■

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Plant development

A bunch of leaves

The intricate and elegant architecture of a flower requires the activity of a plethora of proteins. Many belong to a group of gene regulators known as MADS-box proteins. These form multiprotein complexes that direct the formation of concentric whorls of sepals, petals, stamens and carpels. Gary Ditta *et al.* now show that without the concerted encouragement of four such proteins, all that is produced are clusters of leaves (*Curr. Biol.* **14**, 1935–1940; 2004).

The model plant *Arabidopsis thaliana* has more than a hundred genes for MADS-box proteins. Mutations in some of them produce dramatic effects whereas others have redundant functions requiring double,

triple or even more mutants to uncover their roles. The SEPALLATA (SEP) family fall into this latter category, and earned their name when triple mutants — in which three members of the family were all disrupted — produced flowers made entirely of sepals. With this new work, a fourth sibling, SEP4, emerges.

Ditta *et al.* found that mutating SEP4 alone had no obvious effect, but quadruple mutants lacking all four SEP proteins formed 'flowers' with no recognizable floral organs (as shown here). Closer inspection revealed epidermal cells with the same shape and arrangement as in normal leaves. The presence of branched, hair-like structures called trichomes, a feature of *Arabidopsis* leaves, put this



identification beyond doubt.

In his treatise of 1790, *Die Metamorphose der Pflanzen* (*The Metamorphosis of Plants*), the poet and philosopher Johann Wolfgang von Goethe proposed that flowers were modified leaves. Two hundred years later, stripping away the influence of the SEP proteins has returned them to their foliar state. **Christopher Surridge**