

## Correspondences

# Robust long-term social memories in a paper wasp

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Remembering individual identity is necessary for the complex, individually-differentiated social relationships found in many vertebrates, including humans. Despite the complexity of social insect colonies, individual social insects are generally thought to have simple, undifferentiated relationships. Here we show that *Polistes fuscatus* paper wasps, which individually recognize conspecifics, remember the identity of social partners for at least a week, even if they interact with ten other wasps. Therefore, social interactions among paper wasps are based on robust memories of past interactions with particular individuals rather than simple rules. Considering the small size of wasp brains, these results suggest that at least some aspects of social cognition may not be as cognitively demanding as is generally assumed.

The complex, individually-differentiated social relationships common in social vertebrates rely on individual recognition. Remembering the individual identity of social partners reduces aggression, promotes cooperation, and stabilizes long-term social relationships [1,2]. Given the importance of social knowledge, it is not surprising that the cognitive challenge of remembering the identities, ranks and relationships among many individuals is thought to have driven the evolution of social intelligence in many taxa, including primates and humans [3].

Large colony social insects are on the other end of the social complexity spectrum, as they are thought to lack individually-differentiated relationships. Instead, colony-level social complexity is thought to emerge from the interactions among numerous, cognitively simple individuals following basic decision rules [4]. Recently, individual

recognition has been shown in *P. fuscatus* paper wasps, which use variable visual features (Figure 1) for individual recognition [5], and in *Pachycondyla* spp. ants, which have distinctive hydrocarbon profiles [6]. These studies suggest that previous ideas about social relationships among insects may be overly simplistic.

Individual recognition is typically considered a relatively complex form of recognition because it requires flexible learning and memory. Individuals must learn the unique features of conspecifics, then recall that information during subsequent social interactions. However, prior research indicates that social insects have relatively limited memories; new learning experiences quickly degrade previous memories. For example, honeybees can remember two foraging locations, each associated with a scent, but fail to complete the same task if a third location is tested simultaneously [7]. Considering the size and complexity of social insect colonies, individual recognition

can only produce complex, individually-differentiated social relationships if social memories are sufficiently robust.

We have assessed the extent of social memory in *P. fuscatus* by testing whether memories of past interactions with a particular conspecific are robust to attenuation over the course of a week and to interference from subsequent social interactions with ten other individuals. The strength of memories is predicted to vary with the relative cost and benefits of the memories and may also be influenced by cognitive constraints [8]. For paper wasps, robust memories of prior social interactions would be especially useful given the complex social interactions among nest founding queens. *P. fuscatus* can found nests alone or in groups. When multiple queens cooperate to found a nest, they have intense battles to establish relative dominance ranks. Queens assess multiple nest sites and battle with many potential partners before starting

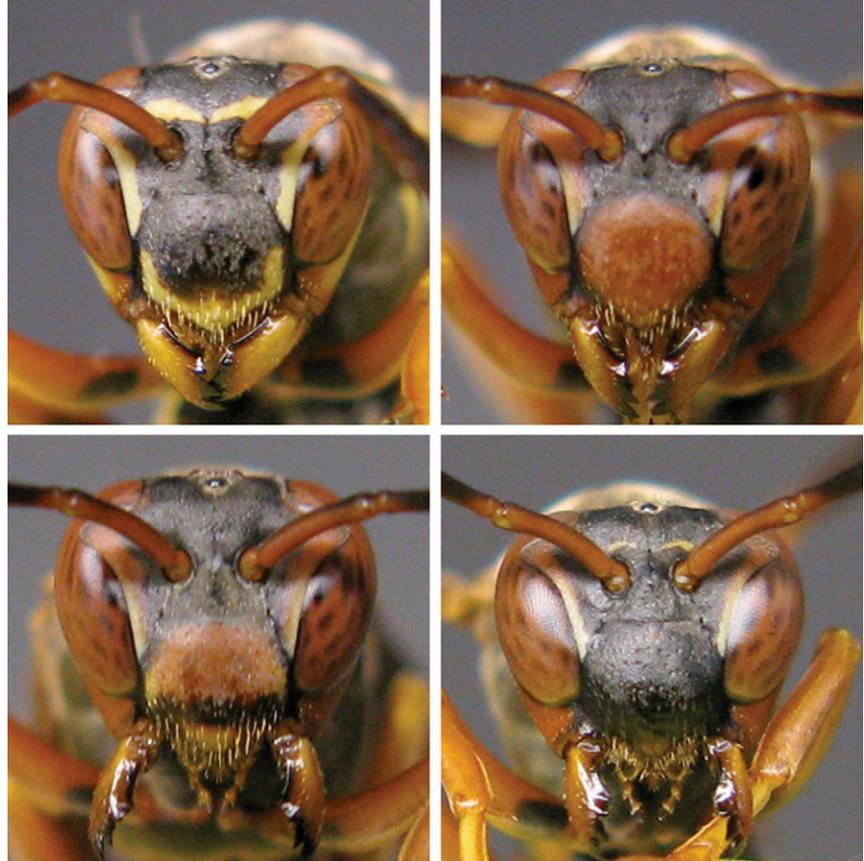


Figure 1. Examples of variable facial patterns used for individual recognition in *Polistes fuscatus*.

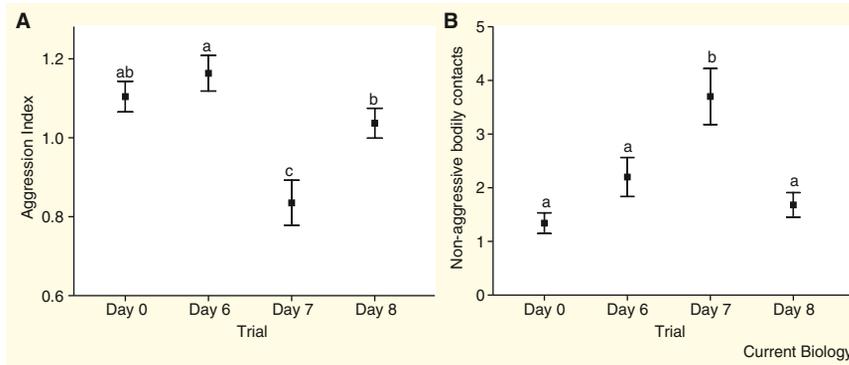


Figure 2. Long-term social memory in a paper wasp.

Wasps were (A) less aggressive and (B) engaged in more non-aggressive interactions with known individuals than with unknown individuals. (A) Aggression indices (Friedman's ANOVA,  $X^2_F(3, n = 50) = 48.10, p < 0.0001$ ) and (B) the number of non-aggressive physical contacts (Friedman's ANOVA,  $X^2_F(3, n = 50) = 21.42, p < 0.0001$ ) for the four days of dyadic encounters between foundresses. The aggression index weights interactions based on the intensity of aggression with lower scores indicating less intense aggression (non-aggressive physical contacts (0 pts) to grappling (4 pts)). On Days 0, 6 and 8 wasps interacted with a new social partner for the first time. On Day 7, wasps re-encountered the same partner from Day 0. Different letters indicate significant differences between days (Non-parametric Tukey's HSD,  $p < 0.05$ ).

a nest [9], so remembering prior social interactions with particular individuals would allow individuals to avoid additional, costly escalated dominance contests. Previous work has demonstrated that *P. fuscatus* are more aggressive to individuals with unfamiliar appearances [5]. Therefore, if wasps have robust social memories, they should be less aggressive towards individuals they have interacted with previously than individuals they have not previously encountered.

Memory was tested by measuring aggression among 50 unrelated wasp queens in four different encounters over eight days ([6] and Supplemental data available on-line with this issue). Initially, wasps encountered a new social partner from a distant collection location (Day 0). Then, we separated the pair, returning each wasp to different communal cages containing ten other wasps. One week later (Day 7), the same wasps interacted again. To ensure that any decreases in aggression on Day 7 resulted from memory of their partner rather than a general decrease in motivation over time, focal wasps interacted with new social partners on Days 6 and 8. If the wasps have robust memories, aggression levels between wasps with prior social histories (Day 7) should be lower than between two wasps that encounter each other for the first time (Days 0, 6 and 8).

Our results demonstrate that previous social partners remembered each other's identities after one week apart even though they interacted with ten other wasps during the intervening time. Aggression indices differed significantly among the days of the experiment (Figure 2A; Friedman's ANOVA,  $X^2_F(3, n = 50) = 48.10, p < 0.0001$ ). Importantly, on Day 7, when wasps were paired with the same individuals from Day 0, the aggression index was lower than all other days (Non-parametric Tukey's HSD,  $p < 0.05$ ). One important reason for the lower aggression indices was that wasps with prior interaction histories (Day 7) engaged in more non-aggressive social behaviors (Figure 2B; Friedman's ANOVA,  $X^2_F(3, n = 50) = 21.42, p < 0.0001$ ). Aggression did not differ between Days 0 and 8, indicating that wasps remained motivated to fight. Therefore, the lowered aggression on Day 7 was due to individual memory rather than a general reduction in focal wasp aggression over time.

*P. fuscatus* wasps therefore remember the individual identity of social partners after one week of interactions with ten other wasps. This is by far the most robust social memory demonstrated in an insect [6]. Social interactions in *P. fuscatus* are not based on simple rule-driven decisions, but on a robust memory of past interaction histories with particular individuals. Robust social

memories are a necessary component of the complex relationships hypothesized to be responsible for evolutionary increases in brain sizes among many vertebrates [3]. So it is interesting that even small-brained invertebrates [10] can form cognition-based social relationships. Perhaps basic components of social cognition may not be as demanding as is assumed by the current formulation of the social intelligence hypothesis. Future research that addresses exactly which aspects, if any, of social relationships are especially cognitively demanding will be important to understanding the role of social complexity in encephalization.

#### Supplemental Data

Supplemental data are available at <http://www.current-biology.com/cgi/content/full/18/18/R851/DC1>

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