

## The role of volatile pheromones in aggregation behaviour in the African social spider *Agelena consociata* Denis

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### Summary

*Agelena consociata* Denis, an African social funnel-web spider, was used to investigate the role of volatile pheromone cues in aggregation behaviour. Sixty-one olfactometer trials were performed, exposing individual spiders to three categories of air currents: those that passed through a subject's own nest, those passed through an unfamiliar conspecific nest, and unexposed currents of compressed air. Spiders were not found to discriminate between their own and unfamiliar nests. Spiders' behavioural responses were found to be affected by the presence/absence of conspecific nests in the airflow.

### Introduction

Pheromones are organic compounds which, when released by an individual, elicit distinct behavioural responses (signalling pheromones) or physiological changes (priming pheromones) in conspecifics (Blum & Brand, 1972). The use of these chemicals is considered one of the primary regulators of behaviour for the social arthropods. However, even in the most intensively studied pheromone system, that of *Apis mellifera*, much remains unknown. The majority of work has concentrated on the chemical composition of pheromones rather than their behavioural correlates (Blum & Brand, 1972).

Pheromone use in spider systems has been noted in drag-line following by male wolf spiders (Araneae, Lycosidae) (Tietjen, 1978), in which spiders locate potential mates by following the pheromone trails left by females on drag-line silk. The web-building jumping spider, *Portia labiata* (Thorell), is a solitary animal that specialises in preying on other spiders and their eggsacs, including conspecifics. *Portia labiata* shows an ability to discriminate its own eggsacs from other conspecific eggsacs (Clark & Jackson, 1994) presumably through the use of pheromones.

Pheromones that require physical contact for transmission have also been identified as functioning for conspecific recognition in colonies of the co-operative spider, *Agelena consociata* Denis (Agelenidae). Krafft (1975) placed anaesthetised *A. consociata* on the colony's web-sheet and sent cricket vibrations through their bodies to simulate the presence of prey. The test spiders were approached as prey items, but the predatory

attacks were abandoned at the moment contact was made. Krafft then washed the integuments of the test spiders with alcohol, an organic solvent, and repeated the experiment. These spiders were attacked and treated as prey.

The use of volatile pheromones by web-building spiders in courtship behaviour has been reported. In the tropical orb-weaving spider *Cyrtophora cicatrosa* (Stoliczka) (Araneidae), airborne chemical cues allow males to detect and locate the position of potential mates (Blanke, 1973). Male sierra dome spiders (*Linyphia litigiosa* Keyserling), in addition to being able to find potential mates, also receive information from the female advertising reproductive status (Watson, 1986).

There are indications that volatile pheromones may play a role in the aggregation behaviour of social spiders as well. Krafft (1970) observed that *A. consociata* cluster in groups when released into a common cage, and suggested that chemical cues underlie this aggregative behaviour. This spider also exhibits the ability to aggregate after forced dispersal in its natural rain forest habitat in Gabon. Roeloffs & Riechert (1988) performed single and multiple releases of *A. consociata* at a common site in rain forest habitat. One third of the nests that formed as a result of this experiment consisted of individuals released in separate trials (i.e. spiders would have had to have located nests following forced dispersal).

We predict that these animals have a mechanism for detecting nearby conspecifics and that this mechanism includes airborne chemical cues.

### Material and methods

In this study we tested for the potential presence of an airborne pheromone associated with *A. consociata* by exposing individuals in an olfactometer to one of three conditions: two pheromone treatments (familiar and unfamiliar nest odours) or an uncontaminated air flow as a control. The test spiders were collected from nests in Gabon, Equatorial West Africa, and brought back to the University of Tennessee, Knoxville. From the moment of collection, they were separated into nest-mate groups and once returned to the U.S. were maintained in an environmental chamber before their use.

The olfactometer consisted of two interconnected chambers through which air was forced at 80 ml/min. The first chamber, or containment barrel, measured 15 × 21 × 29 cm and was constructed of Plexiglass. Nests acting as a pheromone source were suspended in this containment barrel. The second chamber, or bioassay arena, was 9 × 37 × 59 cm (height, width, and length parallel to airflow), also of Plexiglass. Air entering the bioassay arena was first passed through a diffuser to ensure even airflow. The far end of the bioassay arena was fitted with a similar diffuser designed to appear visually and tactically equivalent to the test spiders. The two chambers were connected by approximately 1 m of 1 cm diameter tubing.

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After installing source nests in the containment barrel, test individuals were placed under a brown plastic vial at the central point of the bioassay arena. After a 5-min acclimation period, that served also to flush the system and ensure that air from the containment barrel had reached the bioassay arena, the spiders were released. We scored the spider release as a "positive response" if it moved towards the source nest, and a "negative response" if it moved away from the source nest. If a spider failed to move from the release point within 15 min, it was scored as a "no response".

All trials were done at dusk, corresponding to the daily period of peak activity for *A. consociata* (Krafft, 1970). Spiders were exposed to all three treatments, with the order of presentation randomised. The olfactometer was washed with an organic solvent and clean diffusers installed between trials. We completed 61 successful trials.

Data were analysed in two ways. The general response to different treatments was tested using contingency tables considering all treatments. To test significant choice, sign tests were used. For the second set of tests, the "no response" data could not be tested. This is because a spider not exhibiting a choice has an unknown probability to do so, while given an either/or choice, the expected value can be considered as 50%.

## Results

The average latency for spiders to move from the release point was 11.5 min and ranged from 3 s to over an hour. There were 26% of the animals that sat motionless for more than the 15-min limit.

No significant differences were observed in a spider's response to its own versus foreign nest pheromone cues ( $\chi^2=0.148$ ,  $p=0.93$ ,  $df=1$ ). Therefore, for further analysis all pheromone response data were pooled. Spider response was found to differ significantly between the control and pooled pheromone treatments ( $\chi^2=11.39$ ,  $p<0.005$ ,  $df=2$ ). When data for familiar and unfamiliar nests were pooled, spiders significantly approached a pheromone source (sign test,  $p<0.04$ ) and avoided the uncontaminated control airflow (sign test,  $p<0.04$ ).

## Discussion

Cases where a spider suddenly finds itself away from its nest are not uncommon. Objects falling from the canopy or birds flying through the understory often strike webbing associated with the nest. Spiders are frequently knocked out of the webbing or fall out when attempting to escape (pers. obs.). Spiders can also be carried away from nests by escaping insects. If an insect hits the webbing, and spiders respond to its struggles to escape, a large insect may carry away clinging spiders (pers. obs.).

The mortality rate of solitary spiders finding themselves away from a nest is high. Of 42 marked individuals released into the Gabonese rain forest in areas devoid of established *A. consociata* nests, only two were

found to survive (unpubl. data). In areas where nests were established, survivorship of released spiders was greatly increased (Roeloffs & Riechert, 1988).

Clustered individuals collectively participate in tasks directed at colony survival (e.g. group prey-capture, care and feeding of the young, and web construction and maintenance). Work done on various co-operative spider species indicates that co-operation allows exploitation of larger prey than a single individual could subdue (Brach, 1975; Nentwig, 1985). But more importantly, groups of social spiders need to maintain a minimum web size under conditions that would be too energetically expensive for solitary individuals (Riechert, 1985).

Avoidance of the control airflow may reflect a negative taxis to wind direction and/or a search tactic of this species; by moving "downwind", an individual would position itself such that it would encounter the leading edge of an expanding pheromone cloud from laterally located conspecifics. In any case, a negative response to control conditions strengthens these results under conditions in which a pheromone source is present. We conclude that airborne volatile pheromones are detected by *A. consociata* and that these cues are used in locating conspecifics.

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## References

- BLANKE, R. 1973: Nachweis von Pheromonen bei Netzspinnen. *Naturwissenschaften* **60**: 481.
- BLUM, M. S. & BRAND, J. M. 1972: Social insect pheromones: their chemistry and function. *Am. Zool.* **12**: 553–576.
- BRACH, V. 1975: The biology of the social spider *Anelosimus eximius* (Araneae: Theridiidae). *Bull. Sth. Calif. Acad. Sci.* **74**: 37–41.
- CLARK, R. J. & JACKSON, R. R. 1994: *Portia labiata*, a cannibalistic jumping spider, discriminates between own and foreign eggsacs. *Int. J. comp. Psychol.* **7**: 38–43.
- KRAFFT, B. 1970: Les rythmes d'activité d'*Agelena consociata* Denis. Activité de tissage et activité locomotrice. *Biologia gabon.* **6**: 99–130.
- KRAFFT, B. 1975: La tolérance réciproque chez l'araignée sociale *Agelena consociata* Denis. *Proc. 6th Int. Arachnol. Congr.* (Amsterdam): 107–112.
- NENTWIG, W. 1985: Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae). *Behav. Ecol. Sociobiol.* **17**: 79–85.
- RIECHERT, S. E. 1985: Why do some spiders cooperate? *Agelena consociata*, a case study. *Fla Ent.* **17**: 105–116.
- ROELOFFS, R. & RIECHERT, S. E. 1988: Dispersal and population-genetic structure of the cooperative spider, *Agelena consociata*, in West African rainforest. *Evolution* **42**: 173–183.
- TIETJEN, W. J. 1978: Is the sex pheromone of *Lycosa rabida* (Araneae, Lycosidae) deposited on the substratum? *J. Arachnol.* **6**: 207–212.
- WATSON, P. J. 1986: Transmission of a female sex pheromone thwarted by males in the spider *Linyphia litigiosa* (Linyphiidae). *Science, N. Y.* **233**: 219–221.