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CHEMICAL COMMUNICATION IN VERTEBRATES AND INVERTEBRATES:

EVOLUTION, FUNCTION AND PERCEPTION OF COMMUNICATION SUBSTANCES AND EVOKED RESPONSES

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LA COMMUNICATION CHIMIQUE CHEZ LES VERTÉBRÉS ET LES INVERTÉBRÉS:

ÉVOLUTION, FONCTION ET PERCEPTION DES SUBSTANCES COMMUNICATIVES ET RÉPONSES ÉVOQUÉES

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The Chemical Ecology of Fire Ants: Glandular, Chemical, and Behavioral Parsimony

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Ants occupy virtually every ecological niche on earth and are among the leading predators and scavengers of insects and small mammals. Concomitant with such variety comes tremendous diversity in colony structure and social organization. A large component of ant social organization is mediated by semiochemicals. The fire ant, *Solenopsis invicta*, is a highly evolved ant species that is a serious medical and agricultural pest in the Southern and Southeastern United States. Thus, the driving force has been in place for several decades to understand fire ant chemical communication in an effort to use this information to better control the ant. In fact, more is known about the chemical ecology of *Solenopsis* spp., than any other ant species. Recent advances in fire ant alarm, recruitment, and reproductive pheromones allow us to examine how fire ant exocrine glands, their chemistry, and elicited behaviors have evolved a multiplicity of functions, often context or concentration dependent. The first example is the fire ant alarm pheromone.

Alarm pheromones result in rapid worker searching activities, recruitment of other workers, and sometimes attraction to the source of the pheromone. These behaviors may be useful in making fire ant baits better and more species-specific. The fire ant has several purported sources of alarm pheromones. Crushed heads from workers and worker Dufour's glands produce an alarm reaction used in colony defense (Wilson 1962). The same compounds are involved in fire ant mating flight activities, but in this context the function is no longer defense but promotion of reproductive success. Reproduction in the fire ant begins with synchronized mating flights during which male and female winged reproductives, alates, leave their nests and mate several hundred meters in the air. Just prior to a mating flight, worker fire ants open up holes in the nest surface and swarm excitedly on top of the nest. Male and female alates produce chemical substances that elicit excitement in the worker ants (Obin and Vander Meer 1994). We recently determined the glandular source of chemicals in fire ant alates that cause such excited reactions in the workers. We developed an excitant bioassay and tested body parts and then glandular extracts as dictated by the bioassay results. Our conclusion is that the mandibular glands of both male and female alates cause the observed worker excitement. Further we determined that mandibular gland components in workers and reproductives of both sexes are qualitatively the same; however, the context of their release can evoke mating flights, aggressive alarm, panic alarm, or attraction (Alonso and Vander Meer, In Press). In the future, intra- and inter-specific interactions will be explored, as well as the potential of intervention of fire ant populations through behavior modification.

The sting apparatus of the fire ant is central to the chemical communication of this ant. The venom is composed primarily of piperidine alkaloids that have a wide range of physiological activities, including antimicrobial properties. For humans and other mammals and birds the stings are painful and often plentiful, providing a potent negative associative learning experience. However, more importantly for the fire ant, it has evolved mechanisms to cope with its major enemies, intruder ants. The workers are capable of vibrating their extended gasters while releasing venom from their sting. This results in an aerosol of venom that repels some competing ant species from food resources. If actual combat becomes necessary they can directionally fling droplets of venom at their adversary. Of course, if all else fails they can sting their opponent. In the context of the fire ant nest, workers aerosol small amounts of venom throughout the nest and on their brood (Obin and Vander Meer 1985). The quantities deposited are adequate to have negative effects on entomopathogenic fungi.

The Dufour's gland (attached to the base of the sting apparatus) is the source of the recruitment pheromone of fire ants. When returning from a food source that is too large to carry back to the nest the scout will apply a trail of Dufour's gland secretion through its sting onto the surface on which it is walking. Extracts of the gland elicit a wide variety of behaviors, such as attraction, recruitment (orientation induction), trail orientation, and settling (Wilson 1962; Vander Meer 1986). The chemistry / behavior of these interactions are complex. Each sub-category of recruitment requires a different chemical blend. Z,E-α-farnesene is responsible for 100% of the trail orientation sub-category, whereas Z,E-α-farnesene plus an unsaturated homoeudesmane structure elicits 100% of the worker attraction given by an equivalent amount of Dufour's gland extract. We have only been able to duplicate 85% of the orientation induction sub-category, and that was with a combination of eight Dufour's gland components. In contrast, the related species *Solenopsis richteri*, accomplishes the recruitment process using a single component to elicit 100% of the trail orientation and attraction behaviors. The same compound is responsible for 85% of orientation induction.

Each time the fire ant queen lays an egg, the vulva opens and the sting is fully extended. When the vulva closes, the egg is forced to the base of the sting, whereupon the sting is usually retracted across the egg. This phenomenon has been consistently observed for queens from monogynous and polygynous fire ant colonies. Zero to 4 eggs can be laid for each vulva opening. Multiple egg deposition is more frequent for monogyne queens, and it generally follows an oviposition cycle in which no egg is laid. The egg-laying cycles are evenly distributed during the observation periods, regardless of the total number of eggs laid. This suggests that oviposition is a continuous process in *S. invicta*. We demonstrated that exocrine gland products are deposited on the eggs via the sting. The queen produced worker attractant pheromone and alkaloid antimicrobial agents placed on the eggs give them a survival advantage by eliciting immediate worker care and protecting them from fungi and bacteria in their subterranean habitat. The deposition of queen specific pheromones on the eggs also provides an ideal mechanism for the colony wide distribution of information related to the queen's fecundity, which plays a role in queen/worker regulation of reproduction in the colony (Vander Meer and Morel 1995).

These examples highlight the multiple use of the sting apparatus and the importance of context in the behaviors elicited.

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