

The Fire Ant Sting Apparatus: A Case of Harmonious Parsimony

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The sting apparatus and related glands are of paramount importance to fire ant foraging efficiency and aggressive behavior, both of which also reflect some of the special adaptations of ants.

DEFENSE

Fire ant venom is composed primarily of 2-alkyl or alkenyl-6-methyl-piperidine alkaloids that have a variety of physiological activities (antibacterial and fungicidal). The most cost effective utilization of both workers and venom in defense is to avoid direct confrontation by repelling adversary ants. When disturbed, fire ants can disperse venom through the air by raising and vibrating their gaster in a "headstand" posture. If the intruder is not repelled, the worker can directionally spray venom onto the intruder using another type of gaster vibration called the "aggressive waggle". Fire ants engaged in physical combat have the option of stinging or directly wiping venom on the intruder. Defensively, the fire ant has a hierarchy of behaviors ranging from passive repellent action to aggressive stinging. A corollary to gaster flagging behavior was observed in brood tending workers, who vibrate their gasters and deposit venom on the brood. This behavior helps combat the omnipresent microbes in the ant's subterranean habitat (see Obin and Vander Meer, 1985 for references).

TRAIL PHEROMONE

A trail of fire ants is the end product of the trail pheromone response, which is comprised of a hierarchy of behavioral and chemical sub-categories. The Dufour's gland (attached to the base of the sting apparatus) is the source of the fire ant trail pheromone, and its contents are deposited through the sting onto the substrate by workers returning from a food source. The trail pheromone can be divided into (1) recruitment, (2) orientation primer, and (3) orientation. Workers must first be recruited or attracted to the trail. This is readily demonstrated by the reaction of workers to a point source of Dufour's gland extract. Orientation along the trail is not the automatic next step, since the pheromone component responsible for orientation does not induce orientation in non-trailing workers. An orientation primer or modulator pheromone is required to induce orientation. In Solenopsis invicta these behavioral sub-categories of the trail pheromone are accompanied by distinct blends of chemical components from the Dufour's gland. In addition, large amounts of Dufour's gland extracts induce whole colony migration, and a disturbed individual can release Dufour's gland material to attract and alarm nearby workers (see Vander Meer, 1986).

QUEEN FUNCTION

Female sexuals also have a highly developed sting apparatus; however, they are not aggressive and will not sting even if harassed. Fire ant workers are attracted to their queen, who depends on them for grooming, feeding, and general maintenance. An olfactometer and surrogate queen bioassay was used

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to determine that the attractive pheromone is stored in the poison sac and released through the sting apparatus. This accounts for the queen's well-developed poison sac and it allows her maximum flexibility in the release of its contents. The above bioassays were used to isolate and identify three chemicals responsible for the behaviors defined by the bioassays (see Glancey, 1986).

Investigation of the queen egg-laying mechanism for *S. invicta* revealed that the sting apparatus of the queen is intimately involved (Vander Meer, unpublished). The process begins with partial sting extension and is followed by full extension of the sting and opening of the oviduct. Wave-like abdominal contractions force an egg out of the oviduct and onto a track formed by the sting. The sting is then withdrawn across the egg. Chemical analyses have shown that material stored in the poison sac is deposited on the eggs during the egg-laying process. This can serve at least two functions: (1) The alkaloids in the queens poison sac have antimicrobial activity that can be passed on to the eggs. (2) The queen attractant pheromone, also found in the poison sac, attracts workers to the eggs ensuring them of prompt care (Vander Meer, unpublished). As with workers, there are a multiplicity of functions for the queen's sting apparatus and associated glands.

EVOLUTIONARY IMPLICATIONS

The order Hymenoptera is divided into several sub-orders based primarily on the morphology and function of the ovipositor. The ovipositor of Symphyta took the form of a rasp or saw, and in Parasitica the ovipositor sometimes takes on phenomenal shapes adapted to specific hosts. In both Symphyta and Parasitica the ovipositor is a conduit for egg deposition. In contrast the ovipositor of the sub-order Aculeata evolved into a sting and eggs pass through the female's vulva rather than the sting. The colleterial or accessory glands in other insects are associated with the ovipositor and function to increase in some way the fecundity of the deposited eggs; i.e., promote the adhesion of the eggs to themselves or to the substrate on which they are deposited. These glands were arbitrarily classified as the alkaline and acidic glands, and in Hymenoptera Aculeata they evolved into the Dufour's gland and poison gland, respectively. The above egg laying mechanism indicates that the accessory gland-ovipositor-egg interactions of the sub-orders Symphyta and Parasitica have not been lost in Aculeata, at least not in *S. invicta*.

Multifunctional roles for the exocrine glands associated with the sting apparatus have been reported for other ant species (see Vander Meer, 1983); however, none of them approach the parsimony associated with the fire ant sting apparatus. The multitude of different functions are harmoniously integrated into a finely tuned social insect system.

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