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COMMENTARY: REFLECTIONS ON 40 YEARS

Defining Attraction and Aggregation Pheromones: Teleological Versus Functional Perspectives

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In 1972, three years before the founding of the Journal of Chemical Ecology, John Kennedy in his plenary address to the International Congress of Entomology in Canberra, Australia, offered a challenge to those working with insect attractants—he contended that the "one thing attractants have not been shown to do is attract." Rather, he pointed out that when the odor source was meters or more distant, attractants induce upwind flying or walking along the odor plume, thereby navigating to the odor source. At that time I was midway through my "tenure" as a postdoc with Wendell Roelofs at the New York State Agricultural Experiment Station in Geneva and Kennedy's pronouncement caused me to revaluate how I'd thought about the behaviors evoked by moth pheromones. Not long thereafter, this debate was kindled with the publication of Harry Shorey's wind-tunnel studies at Riverside, showing that male pink bollworm moths could fly upwind in still air along a wind-formed pheromone plume, and that simulation of the visual effects of wind flow by moving a pattern on the tunnel's floor evidently did not influence a male's trajectory. In 1974 Kennedy's group countered with convincing wind-tunnel manipulations demonstrating that an airborne moth deciphered upwind direction by gauging visually how wind modified its trajectory. We now know from further studies with several moths that indeed moths can navigate along discrete plumes under windless conditions, at least over short distances, but that in wind they use visual feedback to detect and head upwind, so-called "optomotor anemotaxis."

Kennedy (1978) was not through with trying to infuse behavior into chemical ecology. In his 1978 review, "The concepts of olfactory arrestment and attraction" he emphasized that both terms were teleological, that is, defined by the endpoints of navigational maneuvers. Kennedy re-emphasized that the term attractant was misleading in this sense, because it implied that the distribution of odor supplied the navigational cue. While such a gradient-dependent mechanism can be used close to the odor source, particularly in still air, movement toward an attractive odor source at a distance is mainly accomplished by detection of upwind direction and using it and the presence of the odor to guide movement along the odor plume. Despite this ambiguity, "attractant" remains a widely used term and clearly it is useful for conveying the end result of such navigation. Unfortunately, simplifying a concept to its endpoint also means that many workers overlook the contribution of the plume's spatial structure to orientation and the importance of visual cues to landing.

Arrestment implies a reduction or cessation of movement caused by an odor or an increase in turning, serving to concentrate individuals in a particular place; often these maneuvers follow orientation to an odor source. In other words, arrestment can follow attraction. Arrestment is not usually defined by the changes in movement that cause it.

Aggregation is an even more vexing concept. At the endpoint level, it simply suggests the accumulation and, perhaps, the persistence of individuals at a fixed location. It too does not directly imply a navigational mechanism, although aggregation presumably is the consequence of attraction followed by arrestment or possibly in a few cases, incidental arrival followed by arrestment. So we can settle on odor-induced aggregation as a readily described phenomenon in terms of an endpoint distribution. The term "aggregation pheromone" is generically applied to a diverse set of behaviors that differ in terms of their underlying orientation mechanisms, and also their behavioral and ecological functions, and the evolutionary forces shaping these behaviors (Wertheim et al. 2005). One convenient distinction is to restrict aggregation pheromones to cases where either both sexes respond or the responder is the same sex as the emitter, thereby excluding conventional sex-attractant pheromones.

Even so, the term aggregation differs widely in terms of delineating the significance of this response to the organism's behavioral ecology. Tristram Wyatt (2014) noted that there are two very different kinds of pheromone-mediated aggregations. First, aggregations can form for the benefits of group living. For example, pheromone-induced winter aggregations of some ladybird beetles (Coccinellidae) facilitate collective defense by amplification of aposematic display, survival over harsh winter conditions, and, come spring, mating.

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Second, aggregations may form in part as the result of eavesdropping, as seems to be the case with the arrival of both females and males of some longhorned beetles (Cerambycidae) to sources of male-emitted pheromone. A male that emits pheromone does so to procure a mate, but the later arriving males are competing interlopers. The temporal persistence of such pheromone-emitting beetles in proximity (in other words, forming aggregations) is not well documented. Capture of males and females at traps baited with pheromone-or host volatiles, however, does not establish that these responders would form aggregations.

Some aggregation pheromones may facilitate mass attack of the host, as seen in some bark beetles (Scolytinae). In this case, one sex produces a pheromone that attracts the opposite sex for mating and cascades into attracting beetles of both sexes. The resulting mass attack weakens the tree and thereby enhances the likelihood that the beetle's progeny survive. Nonetheless, finding a mate precedes host colonization, and the former is a driving selective force in orientation.

Both the cerambycid and scolytine examples differ from sex attractant pheromones in one important respect: both sexes are attracted by a pheromone emitted by one sex rather than only one sex attracting the other. However, the functional roles of aggregation pheromones differ widely. In the ladybird beetle example, both sexes emit the pheromone, the aggregations persist for several months over winter, and mating only occurs when beetles disperse in the spring. The aggregation pheromone promotes clustering in autumn and does not induce mating. In the case of longhorned beetles, male-released pheromone induces attraction of both sexes, resulting in mating and an aggregation that can be relatively persistent at a fixed locus. In bark beetles, the pheromone promotes mate finding and then mass attack of the host tree.

Is there a justification for redefining an aggregation pheromone when this chemical message promotes attraction of both sexes for mating? Its function is very similar to that of a sex-attractant pheromone, with the distinction being that in the case of an aggregation pheromone, as currently used, one sex attracts both sexes. Does the aggregation pheromone label camouflage its function? In some cases, such as the bark beetle example, after mating, females continue to produce pheromone while expanding their gallery. The continued arrival of females and courting males loosely conforms to an endpoint of prolonged spatial clumping. In cerambycid beetles, however, such clustering appears transient, disappearing after mating. A functional redefinition of aggregation pheromone when it is emitted by one sex but attracts both sexes and mate procurement is the primary driving force would be to label it as an aggregation-sex pheromone. This would distinguish between aggregations benefiting group survival with both sexes emitting and responding to the pheromone from aggregations where only one sex emits, both sexes respond, and sexual liaisons are the immediate consequence.

No doubt that the convenience of teleology will continue to influence how we label chemicals that influence behavior and ecology, but we should realize that these terms can hide diverse navigational mechanisms and a multitude of behavioral functions that are well worth understanding. Contributors to the Journal of Chemical Ecology should keep this in mind.

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