

as late as 1957 (161, 168) thought that the returning workers provided additional stimuli (probably tactile) that induced others to follow the odor trail, it is now clear that the trail substance suffices to release the entire follower response (200). The attractant is emitted in invisible streaks. In the fire ant, *Solenopsis saevissima*, the Dufour's gland reservoir contains no more than 0.005 ml of the substance, and a single worker has been estimated to pay out between 4×10^{13} and 2.4×10^{15} mol/cm of trail (204). The concentration in threshold of response was further estimated to fall between 2.4×10^{13} and 1.4×10^{15} mol/ccm. When laid on a glass surface, the fire ant trail substance diffuses to attain a maximum effective width of about 2 cm; the effective diameter then diminishes to zero in about 100 seconds. Wilson's analysis (200) shows that as a result single workers are unable to communicate over distances greater than 50 cm, and longer trails must be built up in chain fashion by multiple workers. An odor trail laid by one worker conveys four bits of information with respect to direction and two bits with respect to distance, or the equivalent of pinpointing one of 16 equiprobable sectors of a compass and one of four equiprobable intervals of a distance scale. Interestingly, this is about the same amount of information communicated with respect to direction and distance by the honeybee waggle dance. The amount of material laid per unit time, as measured by the application time, evidently does not vary greatly with quality or quantity of the food source. This characteristic, plus the rapid evaporation and diffusion of the trail substance, requires the colony to employ "mass communication" in determining the number of workers that go forth. Specifically, the number of workers leaving the nest increases with the amount of pheromone in the trail, the amount of pheromone increases with the number of workers laying trails in unit time, and the number of trail-layers increases with the quality and quantity of the food find. The first studies suggest that among most members of the subfamilies Myrmicinae and Dolichoderinae, as well as in the formicine *Paratrechina longicornis* (Latreille), trail-laying appears to resemble the fire-ant type. In some *Myrmica* and *Lasius*, on the other hand, workers lay visible streaks of material (27, 110). In the case of *Lasius fuliginosus* (Latreille), Carthy (27) showed that the bulk of the "odor spot" comes from the hind gut, but his experiments were not designed to distinguish the action of the pheromone that almost certainly occurs in the trail. Carthy succeeded in disproving (for *Lasius*) the use of a kinaesthetic sense in orientation and polarization cues in the trail, thus refuting the old frequently discussed hypotheses of, respectively, Piéron (126) and Bethe (6), as well as weakening Forel's rather vague theory of the "topochemical sense" [perception of form through odor distribution (53)]. Parallel results were obtained in the study of *Solenopsis saevissima* just mentioned.

Recruitment trail substances, when extracted and tested with the artificial trail assay, have proven to be mostly species-specific, even among species belonging to the same genus (200, 208). No trail substance has