

revealed that the trail laying ant lowers her abdomen, rotates the terminal segment downward and extends her rectal gland. Thus exposed, the gland can just be seen with the naked eye as a white speck on the tip of the abdomen. It is dragged lightly over the substratum, apparently resting on a 'sled' composed of two pairs of long bristles that lead back from the upper edge of the acidopore (Fig. 7). However, this observation alone does not prove that the pheromone comes from the rectal gland. In an attempt to establish beyond a reasonable doubt the anatomical origin of the trail substance, we dissected and prepared extracts of the following body parts, considered to be the most likely repositories of pheromones: rectal gland, sternal gland, Dufour's gland, poison gland, and rectal bladder (which empties directly out of the anus). For the following experiments these organs were freshly dissected from single workers and smeared with the tips of hardwood applicator sticks over the papered floor of arenas to create artificial trails 30 cm in length. The number of workers that followed each trail during the first 5 min was then recorded. From the beginning it was evident that the responses of workers recently motivated by the recruitment efforts of a nestmate were different from those presented with artificial trails without prior stimulation. Accordingly, we conducted experiments in which the workers were first allowed to be antennated by nestmates and then to run along natural trails to honey baits in the arena. Next the baits were removed and artificial trails laid on fresh paper beyond the ends of the natural trails. In order to run parallel experiments in the absence of such motivation, the artificial trails were laid over the same paths on the paper without the intervention of feeding or trail-laying by recruiters.

The results, presented in Table 1, lead to two striking conclusions. First, the rectal gland—and no other part of the hindgut—is the source of the trail substance. It is true that moderate, short-lived following was also elicited by the preparations of sternal, Dufour's, and poison glands. But because the behavior had aggressive components, including raising of the abdomen, opening of the mandibles, and rapid directed movement, we interpreted the activity to be mostly or entirely a response to alarm pheromones in the two glands. This view is consistent with a previous finding that in other formicine genera Dufour's

**Table 1.** The number of workers following a 30-cm artificial trail made from various single-gland preparations. The responses of motivated workers, i.e., those approaching the artificial trails just after encountering a trail-laying nestmate, are compared with the responses of workers not so motivated. Data given are the number of replications (*n*), average number of workers following during the first 5-min period ( $\bar{x}$ ), and the standard deviation of the number of followers (SD)

	Unmotivated			Motivated		
	<i>n</i>	$\bar{x}$	SD	<i>n</i>	$\bar{x}$	SD
Rectal gland	10	0.2	—	5	12.6	5.4
Sternal gland	10	8.2	4.2	5	6.4	4.6
Dufour's gland	10	3.4	2.1	5	2.6	2.2
Poison gland	10	1.5	1.9	5	1.0	2.2
Rectal bladder	10	0.4	1.3	5	1.8	2.2