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19. Supported by a contract with the Division of Biology and Medicine, Atomic Energy Commission, At-(40-1)-2903, and PHS grant MH 11218.

13 May 1974; revised 2 July 1974

Tandem Calling: A New Kind of Signal in Ant Communication

Abstract. Leptothorax acervorum, L. muscorum, *and* L. nylanderi *recruit nest mates to a new food source by tandem running, with only one nest mate being recruited at a time. This technique is initiated by a special "tandem calling" behavior; the recruiter slants its gaster upward and discharges poison gland secretions from the extruded sting. Nest mates are attracted, and as soon as one of them touches the calling ant, tandem running starts. Further details of the full recruitment sequence are provided. Evidence is presented to suggest that tandem running is the evolutionary precursor of odor-trail communication and sex attraction within certain phylogenetic lines of myrmicine ants.*

When a scout ant discovers a new food source or a better nesting site it usually returns to its colony and recruits nest mates to these places. The recruitment techniques employed by different groups of ant species vary considerably. The so-called tandem running behavior is generally considered to be one of the most primitive recruitment methods. Only one nest mate is recruited at a time, and the follower has to keep close antennal contact with the leader ant. This behavior has been described in a phylogenetically scattered array of species, including *Camponotus sericeus* (*1*), *Ponera eduardi* (*2*), *Cardiocondyla venestula* and *C. emeryi* (*3*), *Leptothorax acervorum* (*4*), and *Bothroponera tesserinoda* (*5*), but until recently nothing was known about the precise nature of the signals involved. For *B. tesserinoda* and *C. sericeus* we were able to demonstrate that a recruiting ant first stimulates a nest mate by a special motor display, which we called invitation behavior, before tandem running starts. During tandem running the leader ant and the follower are bound together by a continuous exchange of tactile signals and by a surface pheromone discharged by the leader (*5*, *6*).

Analyses of the signals involved in tandem running of *L. acervorum* have now led to the discovery of a new kind of signal in ant communication, for which we propose the term "tandem calling" (Fig. 1). When a successful scouting forager returns to the colony it first regurgitates food to several nest mates. Then it turns around and raises its gaster upward into a slanting position. Simultaneously the sting is exposed and a droplet of a light liquid extruded (Fig. 2a). Nest mates are attracted by this calling behavior. When the first ant arrives at the calling ant, it touches the caller on the hind legs or gaster with its antennae and tandem running starts (Fig. 2, b and c).

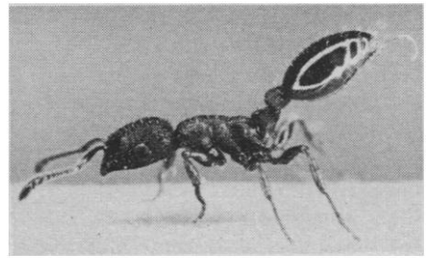

Fig. 1. Chemical tandem calling behavior of a worker ant of *Leptothorax acervorum*. The gaster is raised upward into a slanting position. Simultaneously the sting is exposed and poison gland secretion is extruded.

Table 1. Dummy experiments with *Leptothorax acervorum*. A series of different dummies was presented to tandem followers which had lost their leader ants. Various materials, such as filter paper, were used for dummies. If an ant accepted a dummy and followed behind it, the reaction was considered positive; N = number of trials.

Dummy	N	Positive (%)
Scentless control dummy	10	0
Sting with poison and Dufour's glands	56	100
Gaster without sting glands	126	5.6
Dummy with poison substance	312	100
Dummy with Dufour's gland secretion	69	0

The recruiting ant leads the nest mate to the newly discovered food source. During tandem running the leader ant lowers its gaster, but the sting remains extruded (Fig. 2d). However, it is not dragged over the surface, as it is in the case of ant species which lay chemical trails from their stings. The follower keeps close antennal contact with the leader, continuously touching its hind legs and gaster. Whenever this contact is interrupted, as when the follower accidently loses its leader or is removed experimentally, the leader immediately stops and resumes its calling posture. It may remain in this posture for several minutes, continuously discharging the calling pheromone. Under normal circumstances, the lost follower rather quickly orients back to the calling leader ant and tandem running continues. *Leptothorax muscorum* and *L. nylanderi* show the same tandem calling behavior, with the latter species raising its gaster less conspicuously.

To analyze this interesting recruitment behavior, we attempted first to answer the question: What causes a leader ant to resume tandem calling after it has lost its follower? As mentioned above, if a tandem pair has been separated the leader immediately stops and assumes the calling posture. However, when we touched the ant carefully with a hair at the hind legs or gaster and continued to do so with a frequency of at least two contacts per second, the leader stopped its calling behavior and continued running to the target area. This simple experiment shows that the absence of the tactile signals normally provided by the follower ant is sufficient to cause a leader ant to resume tandem calling.

Second, we asked: Which signals attract and bind the follower to the leader ant during tandem running? The fact that the leader ant extrudes its sting suggested that it discharges a short-lived pheromone, which stimulates the nest mate to follow closely behind. In subsequent experiments we were able to show that the calling pheromone originates from the poison gland. Workers were strongly attracted to dummies contaminated with poison gland secretions, but not to dummies contaminated with secretions of the Dufour's gland. Further experiments revealed that poison gland substance not only functions as a calling pheromone, it also plays an

important role during tandem running by binding the follower ant to the leader. We found that the leader could easily be replaced by a dummy contaminated with poison gland secretions. Gasters of freshly killed ants from which the sting with its glands had been removed could not replace a leader ant (Table 1). However, when they were contaminated with secretions of the poison gland, the dummies functioned effectively as leaders.

Since we found essentially the same recruitment mechanisms in *L. acervorum, L. muscorum*, and *L. nylanderi*, we decided to test the specificity of the calling pheromones. *Leptothorax* (*Mychothorax*) *acervorum* workers were found to respond to the pheromone of *L. muscorum* but not to the *L. nylanderi* pheromone. *Leptothorax nylanderi* workers responded only to the pheromone of their own species. These findings support recent considerations about the phylogenetic relationship of *Leptothorax, Mychothorax*, and *Harpagoxenus* (*7*).

The discovery of chemical tandem calling in *Leptothorax* also throws considerable light on the evolution of chemical recruitment techniques in ants. It now seems very plausible that highly sophisticated chemical mass recruitment, as performed by *Solenopsis* (*8*) and other myrmicine ants, was derived from the more primitive chemical tandem calling behavior of the *Leptothorax* mode. The tandem calling behavior is also relevant to the evolution of sex pheromones in myrmicine ants. It has recently been demonstrated that in several myrmicine species the pheromones originate from the sting glands (*9–11*). It is interesting to note that in species in which wingless ergatoids attract males for mating, for example *Harpagoxenus suble avis* (*10, 12*), the females show sexual calling behavior apparently identical to the tandem calling behavior of *Leptothorax*. This discovery supports the hypothesis that, in at least some myrmicine ants, sex attractants and recruitment pheromones had the same evolutionary origin (*9*).

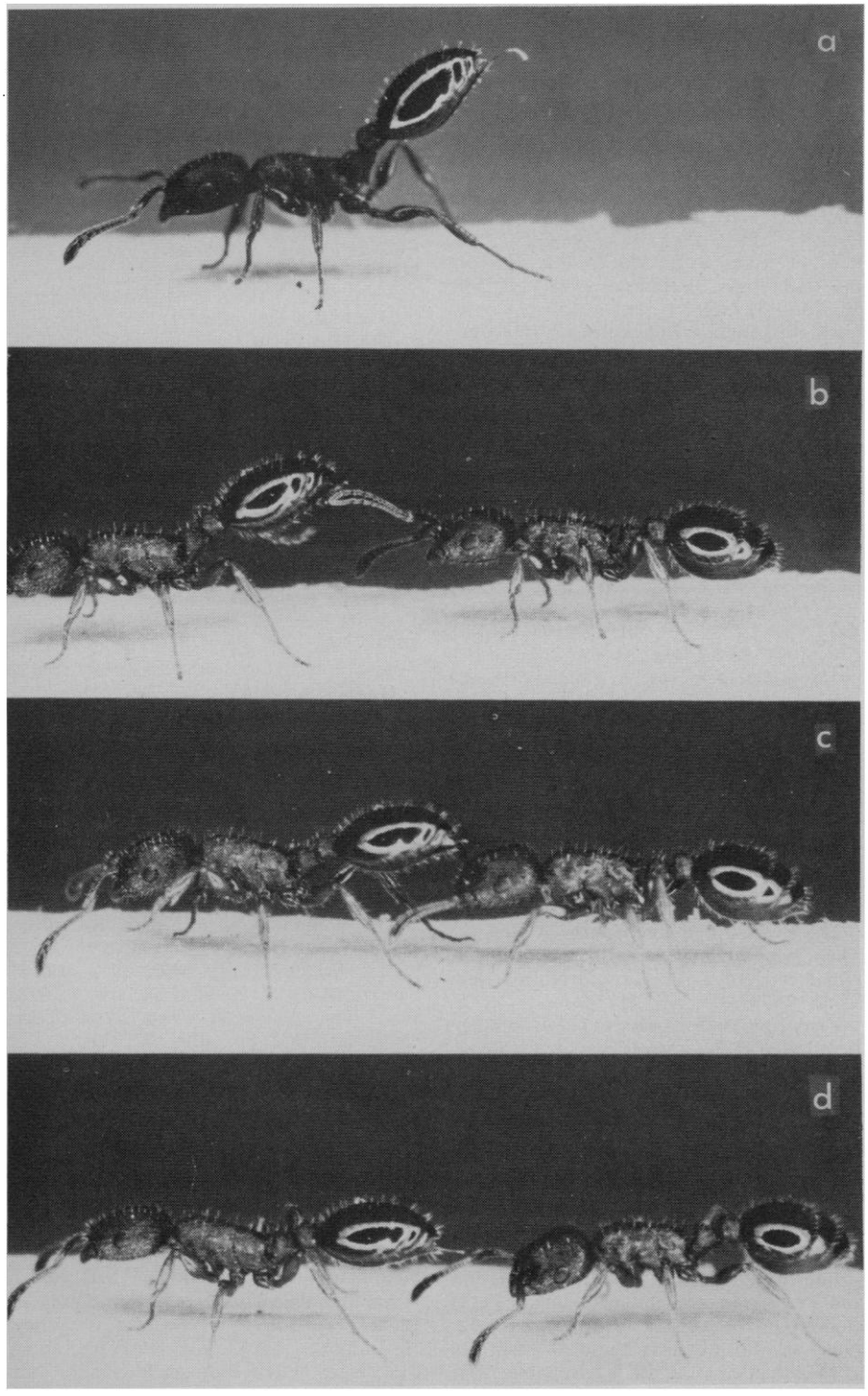

Fig. 2. Behavioral exchange of signals leading to tandem running in *Leptothorax acervorum*. (a) A recruiting worker assumes the calling position. (b and c) A nest mate arrives and touches the gaster (b) and hind legs (c) of the calling ant with its antennae. (d) The calling ant lowers its gaster and tandem running starts. The sting of the recruiting ant remains extruded, but it is not dragged over the surface.

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13. We thank A. Buschinger for his support and E. O. Wilson for critically reading the manuscript. Supported by the National Science Foundation (grant GB 38789 X) and Deutsche Forschungsgemeinschaft (Ho 275).

3 June 1974