

COMMUNICATION DURING NEST-MOVING IN ANTS

Michael Möglich, Arbeitsgruppe Sozioökologie im Fachbereich Biologie der Universität Frankfurt, Germany.

Ants recruit nestmates to newly discovered food sources and to nest sites. For recruitment to food it is sufficient to lead only parts of the colony to the target area. During nest emigration, however, the whole colony has to be moved. This leads to the question: which specific communication signals are employed by ants during nestmoving, and in what way do they differ from other recruitment signals?

In order to analyse the communication during nest-moving it was important to synthesize a complete socioethogram of nest emigrations. In several species we initiated nest emigrations in the laboratory. By marking the ants individually the social organization of nest-moving behaviour could be analysed. I will mainly deal with the analyses of communication behaviour during recruitment to new nest sites.

The most effective and economical technique seems to be mass recruitment by chemical trails. The first quantitative analysis was made by E. O. Wilson (1962). The successful scouts of Solenopsis saevissima discharge a trail pheromone from the Dufour's gland when they return to their nest. This odour trail alone is highly effective and releases trail following behaviour even in the absence of a recruiting ant.

Wilson has shown that the same trail pheromone is used during nest-moving; however, the concentration of the trail substance has to be much higher to release nest emigrations.

Meanwhile, recruitment by chemical trails is one of the best studied methods of communication behaviour in ants. In Camponotus socius a chemical trail functions mainly as an orientational cue. The stimulating recruitment signal is a motor display. Hölldobler (1971) managed to separate the motor signals from the chemical ones. He found that there are two different invitational motor patterns. For recruitment to food sources the ants use a so-called waggle behaviour, whereas for recruitment to nest sites they employ more a 'jerking' movement.

Even more obvious is the significance of motor patterns during recruitment behaviour in species which recruit nestmates by the tandem running technique. This behaviour has been described by Hingston (1929) in Camponotus sericeus and by Wilson (1959) in Cardiocondyla venestula and C. emeryi. We analysed this behaviour in Camponotus sericeus (Formicinae) and Bothroponera tesserinoda (Ponerinae); both species are abundant in Ceylon, and employ the tandem running technique for recruitment to new food places and to new nest sites.

What is tandem running?

When a successful scout of Bothroponera tesserinoda returns to her nest she grasps a nestmate by the head with her mandibles and,

slightly jerking, pulls her back and forth. Then she turns round and offers her gaster to the invited ant. If the invitation is successful the recruited ant touches the scout ant with her antennae. This is the signal for the scout to return to the target area. The scout is now closely followed by the recruited nestmate, which constantly keeps contact with the leader ant by her antennae. If the contact is interrupted and not restored at once, the species act in different ways. The leading ant of Camponotus sericeus waits for several minutes whereas the leading worker of Bothroponera tesserinoda starts her searching runs after a few seconds.

By means of high speed motion pictures we were able to analyse the mechanical signals in more detail. The follower ant holds her antennae on both sides of the leader ant, drumming alternately on both hind legs and the gaster of the ant in front. This mechanical signal informs the leading ant that a nestmate is still following. We were able to simulate this signal experimentally with a hair. If we applied the mechanical contact with a frequency of 2-3 strokes per second, the leader ant continued its progression. The natural frequency is approximately 4-6 strokes per second in both species.

The analysis of the signals connecting the following ant with the leading one is much more difficult. In both species we obtained different results. In our behavioural studies we noticed that the tandem leader keeps her gaster lower to the ground. At first we thought this was to discharge a short-lasting trail substance which releases the following behaviour of a nestmate. We disproved this hypothesis by closing the abdominal tip of 30 workers of a colony (Bothroponera), or even of a whole colony (Camponotus) with collophonium wax. After 24 hours we initiated a new nest emigration. The result was that even ants with closed gasters acted as tandem leaders. Also in tandem running itself there was no difference between treated and untreated insects.

Next, we undertook a series of different dummy experiments to single out the relevant signals. Dummies made from freshly killed workers of Bothroponera tesserinoda as well as parts of their bodies (head, thorax, gaster) were offered in different positions to follower ants. It emerged that these dummies could replace leader ants. The next step was to separate mechanical signals from possible important chemical signals. Therefore we tested artificial dummies made from paper, wax, paraffin and glass-balls. Although these dummies worked when alone, in competition experiments with natural tandem pairs hardly any of them were successful. Only in the absence of a leader ant or a natural dummy, was the artificial dummy accepted.

This suggests that besides a mechanical signal chemical signals might also be important. Therefore we set up some experiments with wax-covered natural dummies and with dummies that were extracted in different solvents. The results suggested that a chemical component was involved. The glands, known to be sources of pheromone, were tested on glass dummies. Compared with untreated dummies they

proved to have no increased value for leading (Dufour-, poison-, and mandibular glands initiate repellent or aggressive behaviour; with hindgut material the ants reacted indifferently.)

However, when we left the glass dummies for a longer time, say 3-20 days, inside the nest their effectiveness proved to be clearly increased. We obtained the same result by applying the eluted dummies with extracts from whole ants, the glands of which had been removed. These experiments identified the effective chemical component as a surface pheromone which is not produced by a distinct gland. This chemical component is not only produced when leading nest-mates but it is present all the time. So it makes no difference whether the natural dummies were taken from leading or following ants or whether they were taken from ants inside the nest. In addition, the pheromone is effective for many hours.

In the tandem running of Bothroponera tesserinoda the following ant is connected to the leading ant by two different types of signals: a mechanical and a chemical one. Both are effective in the absence of the other, but only the combination of both signals guarantees an optimal reaction of tandem following. Only the invitational behaviour determines the motivation of the follower ant to respond to these signals. When we tried, for example, to put together two leading and two following ants taken from different tandems only four out of 25 leader-leader-combinations formed a tandem and no tandem was formed in the follower-follower-combinations.

The main differences in tandem running behaviour of Camponotus sericeus in comparison to Bothroponera tesserinoda are summarised as follows:

1. In Camponotus sericeus the follower ants also respond to dummies. However, in contrast to Bothroponera tesserinoda, the gaster is more effective than head and thorax.

2. In Camponotus sericeus, as in Bothroponera tesserinoda, mechanical and chemical components are important. But in Camponotus sericeus the chemical signal is necessary in any case, whereas the mechanical component has only a complementary function. Extracted and artificial dummies are completely ineffective.

3. Furthermore in Camponotus sericeus the scouts discharge a long-lasting trail substance from the hindgut. This trail pheromone has no recruitment effect. It is used by the scouts as an orientational cue and home range signal. If the optical orientation has been eliminated the ants can be led by natural trails and artificial trails made of extracts from the hindgut.

According to our research, tandem running seems to be one of the most primitive forms of recruitment. Both mechanical and chemical signals are very simple; the chemical signal is not specifically produced for recruiting but is a surface pheromone which is always present. We suppose that it is identical with the so-called colony-odour. In order to add the recruiting signal to the pheromone, the ant that is supposed to follow has first to be motivated. This motivation is achieved by a mechan-

ical invitational behaviour. Furthermore the chemical releaser must be supported by mechanical contact throughout the process of tandem running.

Finally I wish to discuss another method of recruitment behaviour, which seems to be related to tandem running, as far as the success of the recruitment and the grade of its development is concerned. The so-called carrying behaviour has already been described in many species of Formicidae. It has different functions, but it plays an important role during nest emigrations in many ant species. The 'information' about a better nest site and its location is transmitted in a simple and absolutely safe way: nestmates are carried to the new place.

Especially in Formicinae it is remarkable that the fixed motor patterns which initiate tandem running are almost the same as those which initiate carrying behaviour.

When a recruiting ant approaches a nestmate, it shows a slight jerking behaviour, grasps the nestmate's mandibles and pulls her towards herself. As in tandem running the recruiter turns around, but in contrast to the initiation of tandem running, the recruiting ant maintains the tight grasp so that the nestmate is rotated too. She responds by bending her gaster under, and bringing her legs and antennae closely to her body.

By marking individual ants of a whole colony in Formica polyctena and Formica sanguinea I was able to show that the carrying behaviour during nest-moving is organized by a division of labour. In a series of 20 experiments I had the following results. There is a group of workers that in nearly all my experiments organized the nest emigration as carriers. A major part of the colony is very seldom involved in the carrying activity and another large group never carries any nestmates at all. The dissection of the ovaries according to the method of Otto (1958) led us to the conclusion that the carrying specialists are definite 'Aussendiensttiere' while 'Innendiensttiere', -young workers and males-, are carried almost exclusively.

Our results indicate that in some Formicinae, as for instance in Camponotus herculeanus, Camponotus ligniperda and in some Formica species, besides the carrying behaviour, chemical means are employed during nest-moving. In Formica fusca, however, nest emigration seems to be almost exclusively organized by carrying behaviour. In this species only a few workers organize the nest emigration while the main part of the colony stays absolutely passive in the old nest. The following experiment shows the importance of the carrying behaviour in this species:

1. If the specialized carriers are removed from each experiment, nest-moving comes to an end. The colony may even die before other workers start to organize the nest emigration.

2. Instead of just one nest I offered two nests with optimal conditions. I made scouts discover both nests nearly simultaneously and found that now the colony was divided into two parts. Both groups of scouts transmitted their own information by carrying the nestmates to the nest they had themselves discovered.

This again raises the question of how these species recruit to food sources. Do they also use a carrying behaviour, or do they have other

means of recruitment?

We found that Formica fusca uses completely different mechanisms of communication for recruitment to food sources. Whereas specialists carry their nestmates in the nest-moving process in the way already described, their scouts recruit nestmates for new food sources in a way similar to that of Camponotus socius. I found that returning foragers show a very similar wagging behaviour as well as a trail-laying behaviour. Obviously the trail functions mainly as an orientational cue, whereas the waggle display is the stimulating signal to follow the trail. Similar motor patterns during recruitment to food sources have already been described in other species (Leuthold, 1968; Szlep, R. und Jacobi, T., 1967; Szlep-Fessel, R. 1970).

REFERENCES

- BINGHAM, C.T. (1903) The Fauna of British India including Ceylon and Burma. Hymenoptera, Vol. II, Ants and Cuckoo-wasps. (Taylor and Francis, London)
- HINGSTON, R.W.G. (1929) Instinct and Intelligence. (Macmillan and Co., New York)
- HOLLDOBLE, B. (1972) Recruitment Behaviour in *Camponotus socius*. *Z. vergl. Physiol.*, 75, 123-142
- HOLLDOBLE, B., MOGLICH, M. UND MASCHWITZ, U. Communication by tandem running in *Camponotus sericeus*, (in Vorbereitung)
- HOLLDOBLE, B., MOGLICH, M. UND MASCHWITZ, U. (1973) *Bothroponera tesserinoda* (Formicidae) - Tandemlauf als Verständigungsweise beim Nestumzug. (*Encyclopaedia Cinematographica*, Institut für den Wissenschaftlichen Film, Göttingen)
- LEUTHOLD, R.H. (1968) Recruitment to food in the ant *Crematogaster ashmeadi*. *Psyche, Camb.*, 75, 334-350
- MASCHWITZ, U., HOLLDOBLE, B. UND MOGLICH, M. (1973) Tandemlaufen als Rekrutierungsverhalten bei *Bothroponera tesserinoda* Forel (Formicidae, Ponerinae), *Z. Tierpsychol.*, im Druck
- MOGLICH, M. (1971) Nestumzugs- und Trageverhalten bei Ameisen. (Staatsexamensarbeit an der Universität Frankfurt)
- MOGLICH, M., HOLLDOBLE, B. UND MASCHWITZ, U. (1973) *Camponotus sericeus* (Formicidae) - Tandemlauf als Verständigungsweise beim Nestumzug. (*Encyclopaedia Cinematographica*, Institut für den Wissenschaftlichen Film, Göttingen)
- OTTO, D. (1958) Über die Arbeitsteilung im Staate von *Formica Rufa rufo pratensis minor* Gössl. und ihre verhaltensphysiologischen Grundlagen. (*Wiss. Abhandlungen. Deutsch. Akad. Landw.*, Berlin, Nr. 30)
- SZLEP, R. UND JACOBI, T. (1967) The mechanism of recruitment to mass foraging in colonies of *Monomorium venustum* Smith, *M. subopacum* ssp. *phoenicum* Em., *Tapinoma israelis* For. and *T. simothivv. phoenicum* Em. *Insectes soc.* 14, 25-40
- SZLEP-FESSEL, R. (1970) The regulatory mechanism in mass foraging and recruitment of soldiers in *Pheidole*. *Insectes soc.* 17, 233-244
- WILSON, E.O. (1959) Communication by tandem running in the ant genus *Cardiocondyla*. *Psyche, Camb.* 66, 29-34
- WILSON, E.O. (1962a) Chemical Communication among workers of the fire ant *Solenopsis saevissima* I. The organization of mass foraging. *Anim. Behav.* 10, 134-147
- WILSON, E.O. (1971) The insect societies. (Belknap Press of Harvard Univ. Press, Cambridge)