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SOCIAL RESPONSES TO VARIATION IN FOOD SUPPLY AND NEST SUITABILITY IN ANTS (*TAPINOMA ERRATICUM*)

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Abstract. The social organization of *Tapinoma erraticum* colonies has been studied in two environmental contexts: those of mild starvation and of disturbance inducing a complete change of nest site. Trophallactic activity was compared with brood transport behaviour in tests performed repeatedly on the same group of insects. Workers were individually marked enabling interactions to be analysed within the group. An age-dependent difference in behaviour exists during feeding. However, when the colony changed its location, certain workers were found to be transport specialists, whereas others remained inactive: the transport behaviour of *T. erraticum* workers does not appear to be age-dependent, unlike feeding behaviour. A principal components analysis of the results indicated no link between these two types of activities at the individual level. This study indicates the existence of types of social organization which are specific to each of the activities performed.

Our earlier work has dealt with the trophallactic activity of ants (Lenoir 1979a; *Lasius niger*) and their emigration behaviour (Meudec 1977, 1979; *Tapinoma erraticum*). Trophallaxis is the transfer of regurgitated alimentary liquid between colony members (Wilson 1971). Using *T. erraticum*, a species which frequently emigrates in the wild, we decided to combine our methods to determine whether there is a relationship between the behaviour of a given worker in an undisturbed nest and in a nest which has been disturbed. We studied the feeding behaviour of various individuals and compared this with brood transport behaviour when the nest was interfered with.

Several previous studies of ant societies have involved quantitative analyses of individual behaviour (Dobrzańska 1959; Brian 1974; Möglich & Hölldobler 1975; Traniello 1977, 1978). A rather general behavioural catalogue has been described by Wilson for several species of Myrmicinae: *Leptothorax curvispinosus* and *L. duloticus* (1975), *Zacryptocerus varians* (1976a) and *Pheidole dentata* (1976b); 27 to 40 behavioural acts were defined and their frequency of appearance calculated 'in the homeostatic environment of the nest interior'. The author suggested that these frequencies changed as a function of context and also stressed the arbitrary nature of the definition of a behavioural act. None of these authors however, studied the reactions of the same individuals placed in situations as dissimilar as those described below.

Methods

Each group of ants was raised in a 30-cm-long glass tube, 1 cm in diameter, with a water supply at one end whilst the opposite end was closed with a dry cotton plug. The ants were fed with honey and with pieces of *Tenebrio* larva placed near the dry cotton: this position is called the 'fore-nest'. The experiments were performed in an air-conditioned room at a constant temperature of 25 C; lights were on from 0600 to 2000 hours. Each worker was marked using a technique developed in our laboratory. A thin nickel chip with an engraved number was glued on the abdomen of the insect (Verron & Barreau 1974), which was anaesthetized with carbon dioxide during this operation. The ants were not measured, as there is no division of labour related to size in *Tapinoma* (Meudec 1979).

Feeding Behaviour

The groups were starved of protein and carbohydrates for 48 h. The experiment involved the observation with a binocular microscope of exchanges of regurgitated food which followed the introduction of food at the end of the tube. All behaviour related to food sharing was noted: transfers between workers, between workers and larvae, and between workers and the queen. Each transfer was timed. Observations did not last more than 30 min, after which activity diminished considerably.

Nest Transport Behaviour

Before the start of the experiment, the tube in which the group was raised was placed in contact with an identical tube and the water supply was removed. The tube containing the colony was then placed on a hot plate in such a way as to cause a slow and progressive temperature rise to 40 C. The test began when the tube was placed on the hot plate and the movements of each ant were observed with a binocular microscope: displacements into the new tube, the number of loads (nymphs, larvae or eggs) transported, and the number of transports effected. When the transport terminated, the new tube containing the group tested was used to house the group until the following test.

Each group of tests comprised first a feeding test, and second a transport test. The study was performed on colonies founded the preceding summer. Initially each colony included a queen and 10 to 20 workers, as well as 15 to 20 larvae. The populations of these small groups changed constantly as a result of death, laying, development and the hatching of callow workers. Experiment 1 was performed on five colonies given seven weekly tests; experiment 2 on two colonies given 16 daily tests. A total of 177 ants were thus individually studied.

Results

I. Feeding Test

An example of interactions showing trophic flux within a colony is shown in Fig. 1. It can be seen that the level of worker activity is highly variable from high donor activity (worker no. 12) to high receiver activity (no. 21). For this reason, the sequence of food transfer behaviours was analysed (Table I). It appears that when an ant is a donor to a worker, it repeats this behaviour in 84% of following events; receivers show an 80% repeat rate. Thus an ant which just fed another worker is most likely to do the same thing again, but it may give to the queen or become a receiver.

These data led us to classify workers according to their D/R (D = donating, R = receiving) ratios. If D/R is greater than unity, the ant is more of a donor than a receiver and vice versa.

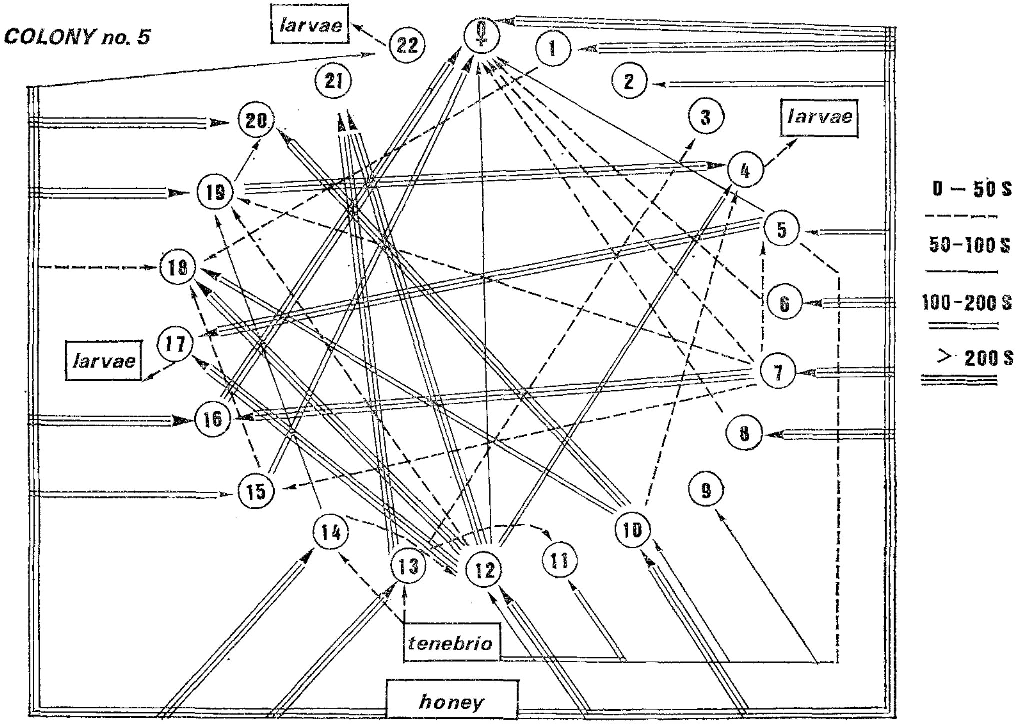

Fig. 1. The durations of trophallactic acts, totalled over the seven weekly tests for colony 5. Trophallaxis is represented by arrows pointing towards the receiving ant or larva. Their thickness is in proportion to the duration of exchange. The time spent by foragers feeding on honey or *Tenebrio* is also represented by arrows.

Table I. Number of Transitions from One Behaviour to Another (Colonies 1 to 5, weekly tests)

Preceding behaviour	Following behaviour DW	DQ	R	No. of transitions
DW	146 83.9%	13 7.5%	14 8%	174
DQ	11 42.3%	9 34.6%	6 23%	26
R	19 7.9%	18 7.5%	192 80%	240
				463

DW: donating to a worker; DQ: donating to the queen; R: receiving from a worker.

In Fig. 2 workers have been ranked according to the level of their donating and receiving activity. The ants were found to fall into three groups: donors, receivers and, between the two, a group of individuals which were in general only slightly active or were low-level donors or low-level receivers. High-level donors are most often low-level receivers and vice versa. Nursing of larvae was not considered here, but it has been shown previously that receivers may also nurse larvae (Lenoir 1979a, b).

We found a strong change with age in trophallactic behaviour, which is similar to that found in many other species (Wilson 1971). In *Tapinoma* most young ants (less than one month old in laboratory conditions) are recipients, while 90% of older ants (more than one month old) are donors, although most of them exhibit a low level of activity (Lenoir 1979b).

A very important regulatory mechanism was observed. When foragers die or there are not enough older workers to feed the colony, foraging and donor behaviour develops early in young ants. When the ratio of young/old workers is greater than unity, some young workers may leave the nest for foraging. This behaviour change is occasionally reversible: in two colonies, young workers ceased foraging after some days and became nurses again when sufficient food was provided (Lenoir 1979b).

II. Nest Displacement Test

Table II shows the number of times an individual transported a load during each test for one of the five colonies given weekly tests. Behaviour of the young workers was noted from the time of their emergence. The results of daily tests are not described here because of their similarity.

In any particular test not all workers are equally active (see Table II). If one considers the results of all seven tests on the same tube, certain workers appear to have a constant level of activity (high or low), while that of others is more variable. At the two extremes in Table II, worker 4 was almost inactive, while worker 1 was almost always active. Of the 21 young workers born during the observation period and observed for at least three weeks, six of them transported on their first test, when they were no more than 6 days of age, and a further nine of them transported on their second test. This indicates that one week of maturation is sufficient for the expression of brood transport behaviour in this situation. One young worker did not engage in transport until after the age of 15 days; five remained inactive throughout the testing period.

The egg-laying activity of the queen in the five colonies and the larval population cycle both cause fluctuations in the number of loads to be carried. It is interesting to ask how work is distributed when the total load varies. Two possible responses to increased colony size are: (i) more individuals might engage in transport; and (ii) those workers which are most engaged in transporting might increase their activity further. Both appear to occur.

(i) The number of transporters increases when the quantity of brood moved increases ($r = 0.40$, $P < 0.02$). The entire worker population, however, is rarely engaged in this activity.

(ii) There were two or more loads per worker in 10 of the 35 cases. In only one case were all the workers active, whilst in all other tests, the excess work was chiefly performed by workers whose activity was high and stable throughout the test period. The most active worker commonly transported more than one third of the total load (e.g. worker 1, colony 4, test 5; Table II). Thus, when the work load exceeded two loads per worker, the number of transporting workers did not increase, rather the activity level of one to four of the most active workers (in a group of about 12 workers) tended to rise.

The duration of the different phases of the transport test varied from one experiment to another. Of the 35 tests in consideration, the alert and exploration phase which precedes the first transport lasted a mean of 290 s (SD = 305). The total duration of the test up to the end of transport had a mean of 418 s (SD = 274). The queen changed nest at the onset of the 'traffic jam' with a mean latency from the beginning of the disturbance of 290 s (SD = 230). She was rarely a transporter: the queen of colony 4 performed one transport in test 5 and two transports in test 7; the queen of colony 5 performed one transport in test 4. All the groups responded with comparable rapidity (in under 10 min) to the same disturbance.

III. Is there a Relationship between the Trophallactic and Transport Behaviours of the Same Individual?

Lenoir (1979b) found an age-dependent behaviour difference in this species, the oldest workers being foragers, the youngest being nurses. We have shown here that, even though certain old workers were capable of moving the brood, most young workers were also capable of this behaviour. Thus a direct relationship between the capacities to show these two types of activity does not appear to exist.

A more detailed analysis of the results was performed using correspondence analysis. This is a form of principal components analysis (Benzecri 1973), which has previously been used to study associations between individuals and

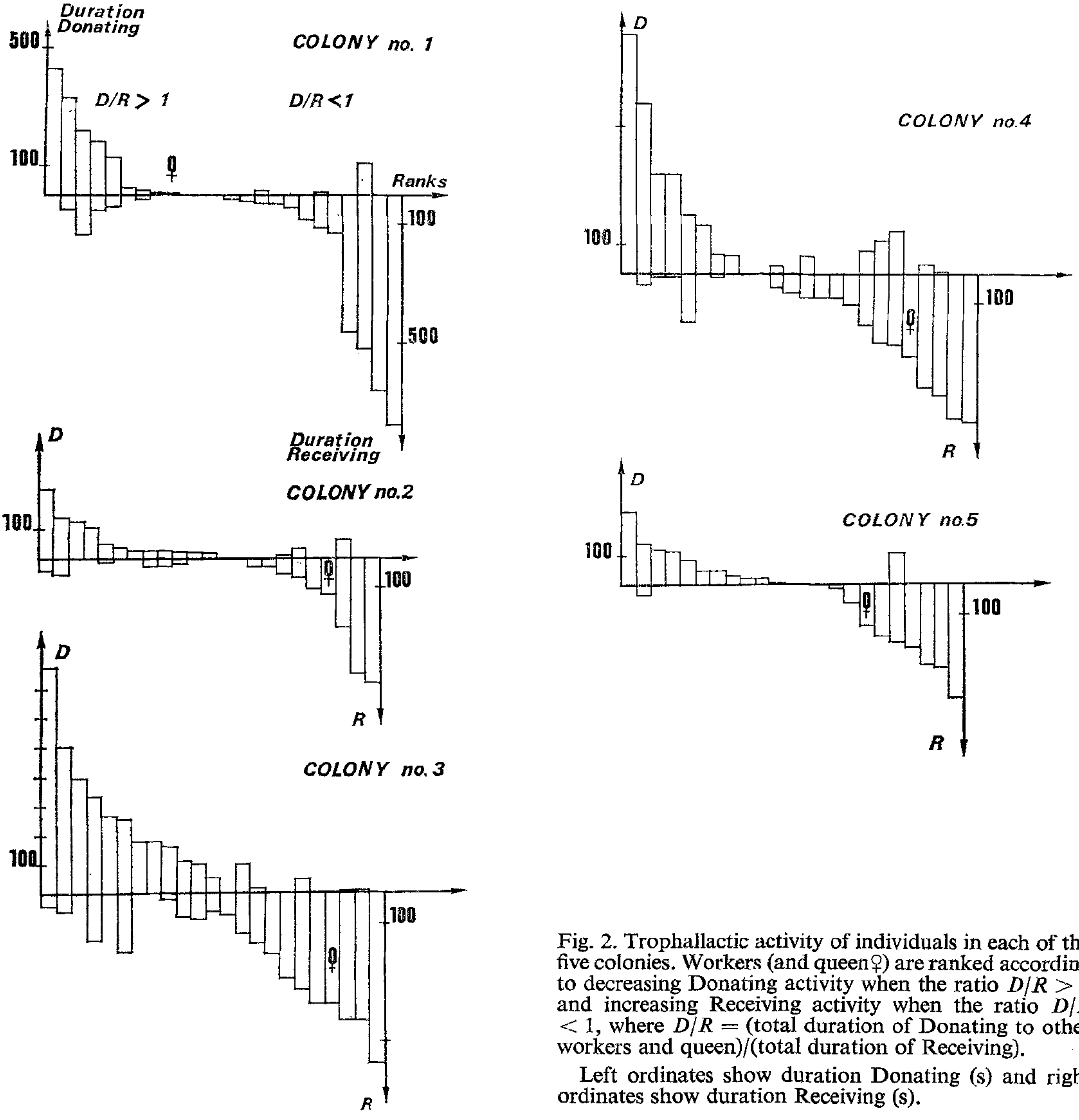

Fig. 2. Trophallactic activity of individuals in each of the five colonies. Workers (and queen♀) are ranked according to decreasing Donating activity when the ratio $D/R > 1$ and increasing Receiving activity when the ratio $D/R < 1$, where D/R = (total duration of Donating to other workers and queen)/(total duration of Receiving).

Left ordinates show duration Donating (s) and right ordinates show duration Receiving (s).

Table II. Frequencies of Carrying Loads in the Nest Disturbance Tests by Individuals in Colony 4 at Weekly Intervals

Ant no.	30 April	6 May	13 May	27 May	4 June	11 June	18 June
1*	0	2	5	1	10	3	2
2*	3	1	1	1	0	0	0
3*	3	0	d				
4*	1	0	1	0	0	d	
5*	0	0	0	d			
6*	0	0	d				
7*	1	10	1	5	d		
8*	1	1	3	1	0	d	
9*	5	2	2	4	0	1	0
10*	1	0	3	2	6	3	1
11*	0	0	1	d			
11′*	0	0	1	d			
12	.	.	.	1	0	1	2
13	.	.	.	3	0	1	2
14	.	.	.	0	2	0	0
15	.	.	.	.	.	2	3
18	.	.	.	.	.	0	1
19	.	.	.	.	.	0	1
20	.	.	.	.	.	0	1
22	.	.	.	.	.	0	2
23	.	.	.	.	.	.	0

*: Old workers (over one month old at the start of the experiment).
d: Workers which died during the previous week.
Workers 12 to 23 hatched during the experiment.

behaviour in *Lasius niger* (Lenoir & Mardon 1978; Lenoir 1979a).

Principal components analysis describes differences between individuals in a heterogeneous sample in terms of a relatively few composite variables called components or factors. The first factor extracts the maximum variance along a single dimension among the individuals in the sample. Each successive factor also extracts the maximum variance remaining but is subject to the constraint of being independent of all previous factors (Frey & Pimentel 1978). Correspondence analysis is a very robust technique because it does not require normal distributions.

In Table III we show correlations between each behavioural act and each factor: these measure the relationship of the original variables to the factors.

(a) **Experiment 1: animals tested weekly.** Table III shows that the first factor represents trophallactic activity between adults, with duration of donating to workers loading opposite to duration receiving from workers (correlations being 0.913 and − 0.953). The second factor represents donor activity towards larvae, and the third factor, donor activity to the queen. We find the number of transports in factor 4, which accounts only for 8% of the total variance. Projection of behavioural acts on the axes for factors 1 and 2 (see Fig. 3) shows that transport is associated with the group of behaviours characteristic of foragers: feeding on the honey and on prey, and giving to the queen and to other ants.

(b) **Experiment 2: animals tested daily.** In these tests we find also transport behaviour in factor 4, but it represents only 1.8% of the total variance (Table III). Projections of behaviours show that this behaviour was exhibited more frequently by receivers: NCM is near to the group of behaviours which characterize nurses (Fig. 4). Thus the weekly tests and the daily tests give different results.

It is concluded from this analysis that:

(1) transport specialists (i.e. ants whose exclusive or principal activity is transport, having no other activity in the nest) do not exist;

(2) the behaviour of most workers during the transport of a brood is not directly related to their behaviour in a situation of normal nest activity; and

(3) whether the most active foragers or the most active receivers generally perform a large number of transports depends on the test situation. Other ants can also be effective transporters.

Table III. Correspondence Analysis of Behaviour by Individuals in Colonies of *Tapinoma*

Behavioural acts	Correlations with Factor 1		Correlations with Factor 2		Correlations with Factor 3		Correlations with Factor 4	
	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2	Exp. 1	Exp. 2
Feed on prey (*Tenebrio*) (FPR)	26	6	0	1	2	−27	1	*−195*
Feed on honey (FHO)	48	165	−61	−14	−14	−3	−37	*−525*
Number of loads carried during migration (NCM)	8	−64	−2	91	0	−1	*−979*	*−476*
Trophallaxis: donor activity (regurgitation)								
Number: donating to queen (NDQ)	79	3	0	*616*	*−355*	19	2	9
Duration: donating to queen (DDQ)	157	11	1	*372*	*−838*	17	2	0
Number: donating to larvae (NDL)	−26	*−178*	*−659*	−17	0	*723*	0	0
Duration: donating to larvae (DDL)	−29	*−443*	*−969*	−27	0	*886*	1	0
Number: donating to worker (NDW)	*449*	*674*	−1	3	9	1	1	−79
Duration: donating to worker (DDW)	*913*	*996*	−1	4	82	0	2	1
Trophallaxis: receiving activity								
Number: receiving from workers (NRW)	*−244*	*−524*	−5	6	0	−27	1	−71
Duration: receiving from workers (DRW)	*−953*	*−992*	44	−1	2	−7	0	0
Eigen value	0.665	0.732	0.422	0.103	0.242	0.078	0.129	0.018
Variance %	42.5	77.0	27	10.8	15.5	8.22	8.3	1.85
Cumulative variance %	42.5	77.0	69.5	87.8	84.9	96.0	93.2	97.85

Experiment 1: 5 colonies, weekly tests.
Experiment 2: 2 colonies, daily tests.
The figures in the body of the Table are correlations between acts and factors (multiplied by 1000). The largest correlations are shown in italics.

Discussion

When the nest is disturbed, *T. erraticum* workers move the brood to a more satisfactory site. There is no precise correlation between the activity of these workers in the normal nest (foragers, nurses, intermediates) and their activity when the brood has to be moved.

Brood transport is characterized by two main behaviour patterns: emergence from the nest, which is normal for foragers, and active seizing of the brood in the jaws, which is normal for nurses. Most foragers were once nurses and so have prior experience in manipulating the brood, but they are not in direct contact with it just before the transport. In spite of this, when the nest was rapidly transported following a disturbance, some foragers took larvae, eggs and nymphs in their jaws and moved them. In the experimental breeding tubes, the receivers did not leave the brood to go to the fore-nest for food. In the case of nest disturbance, they did, however, run out and were also capable of orientation behaviour on a trail. They often performed several round trips between the two nests, transporting eggs, larvae or nymphs.

The response of the colony is thus a function of the situation, and the behaviour adopted by a particular individual in the case of nest disturbance initially appears to depend little on its previous behaviour. The distribution of ants into groups according to their behaviour does not seem to be random: repeated testing shows that, despite response variation, there are consistent differences between some individuals. The experimental conditions may affect the results: for example, daily testing may favour the expression of transport behaviour by nurses, while a weekly test might favour this behaviour by foragers. Following a sudden disturbance of the nest, the reaction of each *T. erraticum* worker may depend on recent experience.

Nest moving behaviour has been studied in several species and a relationship with worker age has been found. The nomad ants (Dorylinae) do not have a form specialized in transport; some young workers transport at their first migration (Schneirla 1971, page 147). Dobrzańska (1973) observed the transport activity of *Formica exsecta* in the field and did not find any age-dependent behaviour difference for this behaviour: she stressed the fact that young colonies of this species have a 'natural tendency' to emigrate. This 'latent migration' behaviour may be compared to that which Wilson (1971) described in *Monomorium pharaonis*, *Tapinoma melanocephalum*, *Iridomyrmex humilis* and *Paratrechina longicornus:* 'Such species resemble the "fugitive" or "opportunistic" species of ecological classifications. That is they depend on finding newly opened sites, exploit them for whatever brief time they are suitable, and quickly move on as soon as the sites become unfavorable'. In species which often move, all individuals and not just a group of specialists may be capable of moving the brood to a new nest. This hypothesis evidently remains to be confirmed by a systematic study. The existence of a group of specialists was demonstrated by Möglich & Hölldobler in *Formica sanguinea* and *Camponotus sericeus* (1974) and *F. fusca* (1975) and it was shown to be composed of certain of the older workers in external service. Herbers (1979), studying *F. obscuripes*, observed that under stress 84% of the transporters are majors. In *Myrmica rubra*, transport is performed by a group of old workers

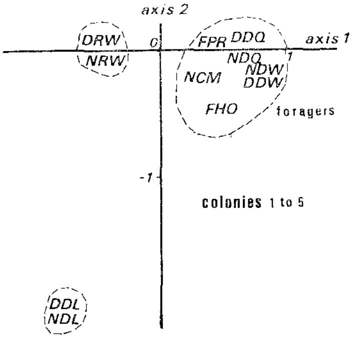

Fig. 3. Projections of behavioural acts on the axes for factors 1 and 2 obtained by correspondence analysis for colonies 1 to 5 (weekly tests). See Table III for symbols.

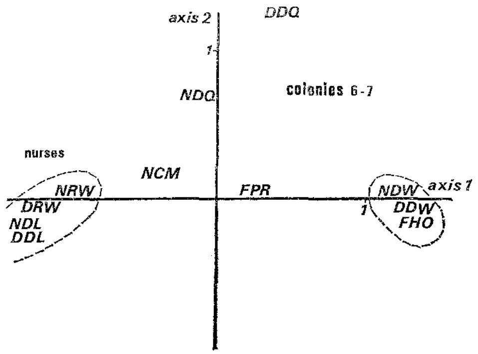

Fig. 4. Projections of behavioural acts on the axes 1 and 2 obtained by correspondence analysis for colonies 6 and 7 (daily tests). See Table III for symbols.

(Abraham & Pasteels 1977). In *Atta sexdens*, the carrying of pupae from one location in the fungus garden to another or from one site to another during emigration is not exclusively performed by a specialized group (Wilson 1980). The absence of transport specialists (to be confirmed by individual marking) could be related to the unique biology of these leaf-cutter ants.

The extent to which individuals differ in behaviour during brood transport thus appears to be species-dependent. It is worth considering the possible effect of the tests used on this type of behaviour. Perhaps an extremely simple external environment, like the one used here, might favour the expression of transport behaviour by certain interior workers which would not be expressed in a natural complex environment. We have found that brood transport behaviour in *Tapinoma erraticum* seems to be only marginally associated with differences in worker behaviour in the nest. In interpreting these results, one should consider the alert situation of the test brought about by an abrupt disturbance, which puts the entire colony in a state of alarm.

It would be interesting to repeat a part of this study, concentrating on the phase immediately preceding true foraging or migratory behaviour. This would be a study of recruiting behaviour in two environmental contexts, since *T. erraticum* workers utilize mass recruitment in both situations. The pioneers guide the rest by means of an odorized trail either towards a food supply or a new nesting site. Thus, Hölldobler (1971) showed that the trail created by *Camponotus socius* was the same during recruitments for food and for emigration. Only the invitation to follow this trail varies: it consists of jerking movements of the recruiting worker during emigration, and of waggles or oscillations during food gathering. Hölldobler & Wilson (1978) also analysed the recruitment system of *Oecophylla longinoda* for food and for a new nesting site, among others. The same type of messages are emitted: a trail from the rectal gland and 'antennation' of tactile stimuli. Added to these are an opening of the mouth and nodding of the head during feeding behaviour, and transport by adults during migratory behaviour. The authors believe that these different types of recruitment provide an example of economy in the use of signals in the evolution of communication systems by social insects.

During a nest move by *T. erraticum* certain workers are active, others not. In tests involving weekly disturbance, the most active workers are apparently most often foragers but, as mentioned above, both experimental conditions and individual experience may affect the results. A more sophisticated analysis will perhaps enable us to show how the disturbing situation is perceived and why the reaction of workers varies independently of their function within the nest.

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