Brood Retrieving in the Ant, *Lasius niger L.*

by

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INTRODUCTION

Some chance observations in the laboratory have shown the existence of a difference between feeding behavior and the retrieving of brood found outside the colony nest. In fact, when smallish colonies are reinforced by the provision of larvae or cocoons, one only needs to deposit the brood on the outside to witness the explorers transporting them rapidly into the nest.

Lubbock (1883, I) used to amuse himself by giving cocoons of *Formica fusca* to foragers in front of his hotel. He observed an ant capable of carrying 187 larvae into its nest in one day.

This behavior is extremely constant since the same insect, after 6 days' isolation in a box, immediately recommenced transporting larvae when placed within 1m of the colony nest. Furthermore, these same workers will carry green-fly eggs inside just as rapidly.

Carthy (1951), Vowles (1952), Wilson (1962, 1976) and Watkins (1964) have observed that brood of various species placed outside the nest is collected rapidly. Several authors used this behavior to test brood recognition, and the signals transmitted; for example: Glancey *et al.* (1970); Walsh and Tshinkel (1974); Bigley and Vinson (1975) (*Solenopsis invicta*); Brian (1975); (*Myrmica rubra*); Jaisson (1972 to 1975) (*Formica polyctena*); Le Moli and Passetti (1977) (*F. rufa*); Robinson and Cherret (1974) (*Atta cephalotes*). Rosengren and Cherix (1981) used pupa-carrying behavior as a taxonomic tool in the *F. rufa* group.

Brood transport when an entire colony is emigrating involves the same motor mechanisms even if the situation is quite different. Colony emigration was observed by early authors and studied by Wilson (1962, *Solenopsis invicta*), Fletcher (1971, *Leptogenys*), Möglich and Hölldobler (1974, *Formica sanguinea* and *Camponotus sericeus*; 1975, *Formica fusca*), Abraham and Pasteels (1977, *Myrmica rubra*) and Möglich (1978, *Leptothorax*). Emigration is cyclic in Doryline ants (Schneirla, 1971). Meudec has studied the transport of brood in small groups of *Tapinoma erraticum* (1973 and thereafter).

Since our studies are concerned with the division of labor, we have become interested in this behavior which has enabled us to set up a test capable of rapidly identifying the foragers in a colony. This test has been described

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elsewhere (Lenoir 1977) but the main results are summarized below.

METHODS AND MATERIALS

Rearing techniques: Animals were reared in an artificial nest represented by a glass tube continuing a watering-trough and sealed with a compressed cotton plug (Lenoir, 1979). The nests were maintained at 25°C. A black mask covered the part near the drinking-trough where the queen, the brood and the nursing ants were gathered. For some experiments, animals were marked with a disk bearing a letter or a figure (Verron and Barreau, 1974). Colonies were fed on honey and *Tenebrio* larvae.

A - Development of the brood-retrieving test.

The test was performed with an initial colony containing a queen and 32 workers (Colony 232, September 1976).

Description of the test: the glass tube, held at an angle of 50-60° to the horizontal with the drinking trough raised, was slowly rotated by hand. The larvae then slid towards the end of the tube and accumulated on the cotton plug which stopped the tube. Normally only larvae and cocoons fell; the eggs and occasional small larvae stayed stuck to the side of the tube. The nest was immediately placed under a binocular microscope and the ants were observed to start brood transport immediately without any intervening latent period. The following criteria were defined:

1°) The number of transporting ants, identified by their number;

2°) The exit order of each transporting ant;

3°) The number of transports performed per individual expressed as a percent of transports (this relative criterion is necessary since from one experiment to the next the number of transports varies).

The time criterion was abandoned because it depends on the number of transporting ants: the duration of a round trip being more or less constant. If the total number of transports was less than 50, the experiment was immediately repeated a second time so as to observe at least 100 transports per test.

At the same time, a certain number of observations were made on feeding behavior. The object of this was to see if any correlation existed between feeding and brood-retrieving. If a panic situation was accidently created, for example dropping the tube, then the experiment was immediately terminated. If the queen falls to the front part of the nest with the brood, she is not brought back first. The female is licked by the carriers who touch her with their antennae, but the larvae are retrieved first before the queen is pulled, subsequently to move by her own efforts.

If the colony has been starved for several days and if food and larvae are placed simultaneously at the nest entrance, normally the food is preferred but there are exceptions. If the experiment is repeated using bodies of dead ants killed a few minutes previously and also brood, then the corpses are ignored while the brood is transported. The corpses are moved into the colony about 1 hour later.

RESULTS

Recruitment: As the number of transporting ants increases very rapidly, a method of recruitment must exist. The worker leaves its larva at the extremity of the region where the brood is to be found and leaves immediately. This behavior is different from that observed in the case of food recruitment where the forager actively solicits some nestmates with movements of the antennae (invitation behavior). Often, a worker who has stayed near the queen fetches the larvae and puts it in the center of the brood. The number of transporting ants progressively stabilises to a level which varies from test to test: 10 to 16 (31 to 50% of the colony workers - Fig. 1). The number of individuals having transported at least once over the five tests was 24, that is 75% of the total. Thus the potential number of transporters in a young colony is very high. Carthy (1951) showed that when the brood of *Lasius* is brought back to the colony, visual clues are used, and a trail is laid. The visual clues are perhaps more important than the trail in orienting the animals, but the author does not deal with recruitment. Wilson (1962) has confirmed the existence of a trail in *Solenopsis* which facilitates recruitment; the recruitment curve is parallel to that observed for a source of food. In this species, chemical recruitment alone is effective whereas in *Lasius niger*, invitation behavior plays an important part in recruitment to a source of food. There is no difference between the two types of recruitment, invitation behavior simply increases the effectiveness of the trail. In the case of the brood-retrieving one may imagine, although this has not been shown, that the carriers lay a trail which stimulates recruitment without invitation.

Stability of the behavior: In order to estimate the stability of transport behavior the percentage of insects transporting twice in succession was calculated, bearing in mind that the tests were repeated 5 times at 2-3 day's interval (Table 1). This was found to be between 33% and 60%. The behavior thus fluctuates and different workers may be transporters from one day to another.

This phenomenon may also be demonstrated by the asymmetric matrix of the exit order on day 1 and that of day 2. A stable exit order (maximum

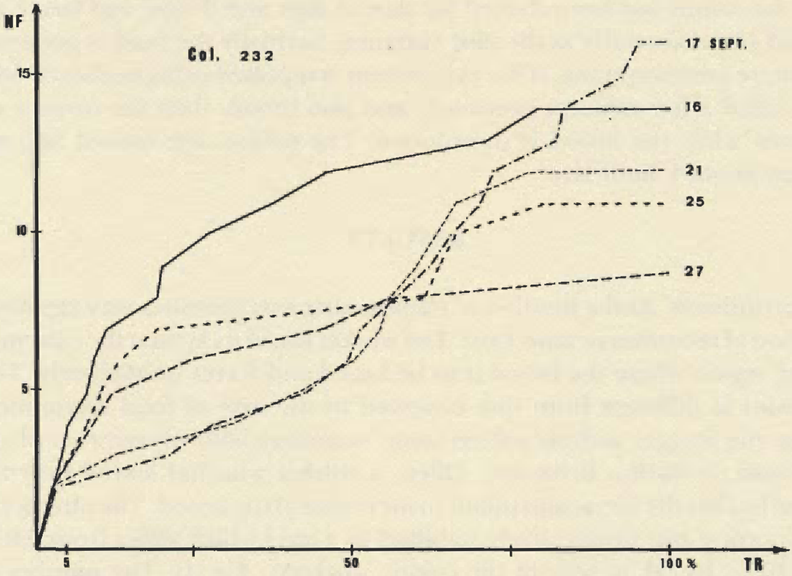

Fig. 1. Recruitment during brood-retrieving experiments in colony 232
NF = Number of carrier ants
TR = Cumulative % of transports

Table 1. Rate (%) of workers transporting brood twice in succession.

Test Number	%	Number of ants
1 ⟶ 2	52,6%	19
2 ⟶ 3	33,3%	20
3 ⟶ 4	46,7%	16
4 ⟶ 5	61,5%	13

change of 1 in the exit order) was found in only 18% of the cases examined.

Very active insects (more than 10% of all transports) and stable carriers (carriers in at least 4/5 trials) are rare compared to the total population, 3 in the case of colony 232 (4% of the total number). These results are in close agreement with those of Verron (1976) who used the same species. This author found that only 14% of the workers showed a high level of locomotor activity, stable for 3 weeks. In *Tapinoma*, 10% of the workers are permanently active during a 10 day brood transport (Meudec, 1973 a). This small number of individuals represent the "elite" of the colony (Oster and Wilson, 1978).

Exit order and number of transports: A negative correlation was found between the animal's mean performance in the 5 tests and their median exit order position ($r = -0.755$, $P < 0.01$). This means that the ants which exit first carry out the greatest number of transports, that these animals are very active and stay so until the task is completed.

Relationship with the foraging-behavior: Tests of brood-retrieving were carried out following observations on feeding behavior (3 observations each lasting one and a half hours). 58% of the ants in the first test were both carriers and foragers. If one summarizes tests results in the knowledge that an ant can be exclusively a carrier one day and solely a forager in another test, then the number of individuals having displayed both types of activities is 84%. Ants that are only carriers are extremely inactive, 0.8% of the transports at the most. The same thing is true of the animals that are only foragers, 0.4% of those exhibiting food searching activity (measured by the total duration of alimentary exchanges). Thus one is able to identify 80% of the foragers in a colony by three short tests of brood-retrieving behavior.

A search was made for possible correlations between the activity of brood-retrieving (the number of transports) and the activity of foraging measured by two criteria (using base two logarithmic coordinates).

a- the time spent in the fore-nest estimated by a sampling method: the numbers of ants foraging in the fore-nest was noted every 5 minutes and we calculated the percentage of presence in the fore-nest.

b- the duration of regurgitations, otherwise known as donor activity. For the number of transports and the time spent in the fore-nest the correlation is low but significant ($r = 0.431$, $P < 0.05$).

The same thing was true of the correlation with regurgitation activity ($r = 0.4651$, $P < 0.05$). A much stronger correlation was found between regurgitation activity and the time spent in the fore-nest ($r = 0.5882$, $P < 0.01$). This means that the foragers which are best at providing food (those which regurgitate a lot) stay the longest in the fore-nest and they are at the same time the best in brood-retrieving activity. These individuals carry out the largest part of the task of providing food, in excess of 98% taking as criterion the total length of trophallaxis.

To study the correlations between the brood-retrieving and other forms of social behavior a correspondence analysis was performed on data obtained from colony 232. Correspondence analysis is a particular type of principal components analysis (Benzecri, 1973). Its application to the analysis of division of labor has been explained elsewhere (Lenoir and Mardon, 1978). The following variables were obtained:

- for regular surveys on the fore-nest: forage, feed on honey, feed on the prey, and for regular surveys on the brood: stand on the brood.

- for the number of acts: the number of transports and lickings of larvae in the nest (brood-care); brood-retrieving inside the nest, the number of regurgitations to the queen, to the larvae, or to other ants, and the number of receptions (solicitor activity).

- for the duration of trophallactic acts: the time spent in regurgitating to the queen, to other ants, to larvae and the time of receiving activity.

The results of this analysis are shown in table 2 and in figures 2 and 3. It appears that the first factor contrasts the behavior of foragers with that of receivers. The second factor allows one to distinuish the receivers that are nursing larvae. The third factor also describes the foragers. These are ants which go to the fore-nest, feed themselves, and retrieve the brood. About 50 colonies were studied in this manner and the relationshp between foraging behavior and the brood retrieving behavior was always confirmed.

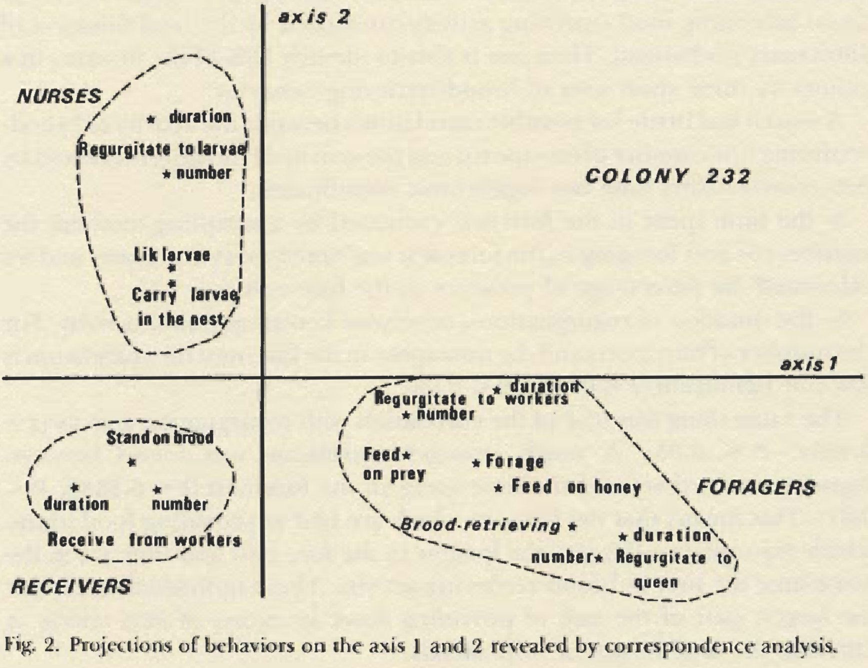

Fig. 2. Projections of behaviors on the axis 1 and 2 revealed by correspondence analysis.

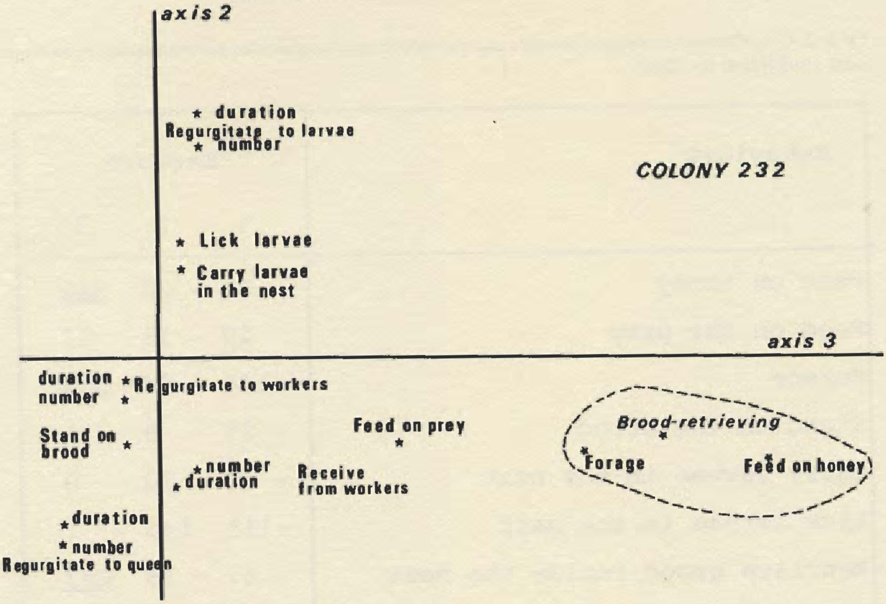

Fig. 3. See Fig. 2: axis 2 and 3.

B - Free choice experiments

Description of experimental protocol: It is of interest to see if the carriers preferentially retrieve such or such element of the brood. It is difficult to do this using the test described above because the amount of brood varies between colonies. The following method was chosen: 20 elements of brood were distributed in a 7 to 10 cm long glass tube which was placed in close contact with the colony. This is a real choice situation. An ant is confronted with two dissimilar brood components, for example a big larva and a little larva or a little larva and an egg. The order of transports is scored from 1 to 20. If the first transports corresponded to one single category of brood, the minimum score is 55 out of a total of 210. Statistical analysis were performed using the Mann Whitney U test. If the sum of ranks of transports from the category which obtains the best score is less or equal to 74, this corresponds to the 1% probability level; if it is between 74 and 82, this corresponds to the 5% level and beyond that the choice is not significant. $\bar{X}$ is the mean and s is the standard deviation (° : significant with $P < .05$ and °° significant with $P < .01$)

In all these free choice experiments, the ants were not individually marked.

Table 2. Correlation between behaviors and the first factors revealed by correspondence analysis (data multiplied by 1000).

Behaviors	Factors		
	1	2	3
Feed on honey	88	- 26	616
Feed on the prey	29	- 15	87
Forage	144	- 34	552
Stand on the brood	- 25	- 9	- 1
Carry larvae in the nest	- 57	70	0
Lick larvae in the nest	-115	146	- 1
Retrieve brood inside the nest	67	- 18	823
Trophallaxis : donor activity			
Regurgitate to the queen : Number	52	- 15	- 6
Regurgitate to the queen : duration	65	- 15	- 6
Regurgitate to larvae : Number	- 97	623	6
Regurgitate to larvae : duration	-168	821	6
Regurgitate to workers : Number	414	- 32	- 56
Regurgitate to workers : duration	953	- 3	- 35
Trophallaxis : sollicitor activity			
Receive from workers : Number	-105	-139	4
Receive from workers : duration	-700	-295	- 3
Eigen Value	0,527	0,269	0,170
Variance %	44,7	22,8	14,5
Cumulative Variance %	44,7	67,4	81,9

RESULTS

1) Choice between brood from the colony or from a strange colony of the same species.

Workers can recognize their brood from brood of other species (Jaisson, 1975; Brian, 1975; Meudec, 1979). The question posed was whether they can recognize brood of the same species as belonging to another colony. These choice experiments were first carried out in summer and then in autumn.

a) In summer (July-August)

1st experiment: 10 larvae from original colony, 10 larvae from foreign colony. All larvae were medium sized. The test was repeated 5 times.

The rank sums for transport of larvae of the original colony were as follows: 107, 102, 101, 104, 91, $x = 101$ and $s = 6.041$. Each colony was tested once to eliminate familiarisation problems with foreign larvae. At no time was one or other type of larva significantly preferred to the other (Mann-Whitney U test). The larva stimulus is thus very powerful and non-colony specific.

A contingency table was established (Table 3) and a X^2 test confirmed the above result.

2nd experiment: Using one colony, the experiment was repeated 10 times (over 10 consecutive days). Leaving 10 strange larvae each time. The rank sums for transport of larvae from the original colony were as follows:

91, 85, 79°, 83, 82, 78°, 101, 87, 78°, 72°,

$\bar{x} = 83.6$ and $s = 8.113$

A significant choice was obtained in 40% of the tests. A comparison of the numbers of familiar and strange larvae carried during the 10 first and the 10 last transports yielded a X^2 of 4.5 ($P < 0.05$). This confirms a preference for larvae from the colony of origin (Table 3).

3rd experiment: In this trial, a free choice between 10 cocoons from the original colony and 10 foreign cocoons was presented 10 times over 10 consecutive days. Rank sums for transport of cocoons from the colony of origin were:

72°, 111, 92, 85, 86, 74°, 97, 91, 87

$\bar{x} = 88.7$ and $S = 11.116$

Although these results are less clear-cut than the preceding ones (only 20% significant trials), the X^2 calculated using the 10 first and the 10 last transports was significant ($P < 0.01$, table 3).

b) At the end of the season (October)

Table 3. Choice tests between brood native of the same colony or of a strange colony. Data represent the number of loads carried during the first 10 (1 to 10) or the last 10 transports (11 to 20) °°:$P < .01$

	10 successive tests				1 test by colony			
	Larvae		Cocoons		Larvae		Cocoons	
Rank of transports	1-10	11-20	1-10	11-20	1-10	11-20	1-10	11-20
Brood native from a strange colony	42	58	40	60	85	25	26	24
Brood native from the same colony	58	42	60	40	25	85	24	26
	χ^2=4,5°°		χ^2=7,22°°		χ^2=63,29°°		χ^2=0,04 non significant	

11 experiments were carried out with different colonies according to the same experimental design: a choice between 10 familiar and 10 unfamiliar larvae. The rank sums for transports of larvae belonging to the original colony were as follows:

103, 63°°, 65°°, 74°°, 80°, 82°, 55°°, 94, 74°°, 83, 56°°

$\bar{x} = 75.636$ and $s = 15.692$

A significant preference for larvae from the original colony was evident in 73% of the cases ($X^2 = 63.29$, $P < .01$) and was seen in the first test in contrast with the tests in series a.

It was noticed that larvae taken from colonies in October were yellow, shrunken and not very turgid. These are hibernating larvae. If foreign larvae are given to a colony, they are taken by foragers as described above, but, they are not adopted immediately by the nursing ants who may drop them provisionally on the waste pile, or lose them in the nest.

Table 4. Time necessary for adoption of wintering strange larvae.

	Number of larvae	1hour after Number of larvae rejected	2hours after Number of larvae adopted
Colony n°1	48	26 54,2%	all
Colony n°2	39	19 47,7%	all
Colony n°3	74	41 55,4%	all

Table 4 lists the results of observations made in October on 3 colonies of labelled ants. All the foreign larvae were adopted after approximately 2 hours. They were placed with the brood and licked like others.

A crowd of workers proceeding in the opposite direction was also noted: some were carrying larvae towards the pile of waste and others were carrying the larvae towards the colony. A systematic enumeration was carried out for colony n°3. At the time of peak activity, 21 journeys to the brood and 14 to the waste pile were observed in a 5 minute period. This explains how all the larvae were finally adopted.

Individual variation in this behavior is evident from the data presented in table 5. Out of 17 ants, 7 adopted larvae, 8 rejected them and 2 others performed 2 types of transports. It seems that nursing ants within the colony perceive the stimulus of strange, hibernating larvae differently. Some consider it as a foreign element to be rejected while others take it as an object to be cared for.

CONCLUSION

In a free choice situation using 10 larvae (or cocoons) from the colony of origin and 10 larvae (or cocoons) from a strange colony, the first ten objects brought to the nest were chosen at random in the first test carried in the middle of the season, but brood of the colony of origin were preferentially selected in the following tests. The same preference was observed from the first test onwards at the end of the season. This may mean that summer brood no matter what their origin is attractive to foragers but the workers learn to

Table 5. Individual variability in carrying behavior during adoption of wintering strange larvae (colony n°3). Data represent the number of transports during 30 minutes.

worker n°	Number of transports towards brood (adoption)	worker n°	Number of transports towards wastes (rejections)
29	31	35	7
21	5	72	10
75	5	25	11
65	19	2	1
17	1	32	1
47	12	22	13
66	4	1	5
26	2	26	1
45	1	45	4
		55	9
	total 80		total 62

recognize foreign brood after a few days. At the end of the season, however, the larvae enter hibernating diapause and the foragers are immediately able to recognize their own larvae.

2) Choice between different components of an unfamiliar brood.
The following choices were proposed:
- large (La) vs. small larvae (l)
- large larvae (La) vs. cocoons (Co)
- small larvae (l) vs. eggs (w)

Either 10 (La - l choice and La - Co choice) or 11 (l - w choice) trials were performed. The results were analysed in the same way as above, using a X_2 test on the 10 first and 10 last transports.

Table 6 shows that large larvae and cocoons were clearly preferred to small larvae and eggs which were transported last of all. Eggs were even ignored on occasion. Carriers often put down an egg to take a small larva, and would

Table 6. Number of loads carried during the first 10 or the last 10 transports and sums of ranks (SR) for the preferred load.
°: $P<.05$; °°: $P<.01$
Choice La/1 70% significant preferred La
1/w 82% significant preferred 1
La/Co 10% significant preferred Co

Choice		Rank of transports	
		1-10	11-20
Large larvae	La	74	26
VS small larvae	1	26	74
SR La = 93-69°°-84-57°° 54°°-121-79°-65°°-57°° 58°° $\bar{x}=73{,}7 \pm 21{,}1715$		$\chi^2 = 44{,}18^{\circ\circ}$	
Small larvae	1	82	18
Oeufs	w	18	82
SR 1 = 56°°-61°°-54°°-59°° 55°°-91-76°-89-56°°-70°°- 69°° $\bar{x}=66{,}909 \pm 13{,}4496$		$\chi^2 = 79{,}38^{\circ\circ}$	
large larvae	La	55	45
Cocoons	Co	45	55
SR Co = 114-70°-114-86-83- 117-106-115-91-111 $\bar{x}=100{,}7 \pm 16{,}7468$		$\chi^2 = 1{,}62$	

explore the entire tube for the last larva before starting on the eggs. Similarly, when the choice was between large and small larvae, ants would change their load in favor of the large larvae, but with large larvae and cocoons, collection occurs at random and starts with the object closest to hand. It seems as though large larvae and cocoons are located more easily; small larvae and eggs are taken when touched by the antennae. The large larvae or cocoon stimuli are very strong. This is reminiscent of slave ants who carry large larvae or cocoons of the slave species at random (see for example Wilson, 1975, *Lept. duloticus*). For Elmes (1977) "larvae have evolved mechanisms that make them more attractive to the workers; these mechanisms are usually more developed in larger larvae, ensuring them a larger share of the colony's resources than smaller larvae." This phenomenon was observed by Brian (1957) in *M. rubra*, and we found the same result in *L. niger* (Lenoir, 1979). We must except queen-biased female larvae which are less attractive and treated with hostility (Brian, 1973, a, b). In many species large larvae and pupae are treated differently: in *M. rubra* pharate pupae are picked up in preference to pupae (Brian, 1975). In *Solenopsis* (Walsh and Tshinkel, 1974) and *Neivamyrmex* (Watkins and Cole, 1966), it appears to be the other way round. When colonies emigrate, further contradictory evidence has been found. Dobrzanski (1966, *Leptothorax*) and Meudec (1973, b, *Tapinoma*) found that pupae were carried first, while Le Masne (1953, *Ponera*) and Gupta (1966, *Oecophylla*) found that larvae were left in preference to eggs and small larvae. It is even possible that workers cannot tell the difference between small larvae and eggs since the former are left on the egg pile as long as they have not moulted (Walsh and Tshinkel, 1974; O'Neal and Markin, 1973; Le Masne, 1953; Weir, 1958). However, according to early, contradictory observations by Fielde (in Raigner, 1952), the small larva of *Aphaenogaster* is fed as soon as it hatches from the egg.

C - Influence of larvae deprivation on the choice of brood-retrieving.

Young ants were raised with the queen but in the absence of larvae. Eggs laid by the queen were removed every 4-5 days such that workers had no contact with larvae since hatching.

1st experiment: 4 colonies composed of a queen and 40 workers hatched on the same day were used. Workers were subjected to a small larva/egg choice test when 15 days old. It is known that foragers (generally old workers) definitely prefer small larvae to eggs, which are occasionally abandoned (see above). A check was made that this behavior exists in a colony of workers of identical age. The test was carried out in 3 stages using unmarked workers.

- 1st test: 10 larvae/10 eggs choice, the brood was removed immediately following the test
- 2nd test (24h later): As above but the brood was not removed
- 3rd test (24h later): Same choice

It is necessary to note that in the first test workers familiar with eggs only were used, whereas in the second test, the same workers were used after a very brief (<1h) time in contact with larvae. In the third test, workers familiarised with larvae for 24h were employed.

RESULTS

Table 7 shows the rank sums for larvae transport (SR) and the number of larvae (n 1) carried from the 1st to the 10th transport. X^2 was calculated for the 4 colonies together using a 4-way contingency table: carriage of 1st to 10th and 11th to 20th load.

It is quite plain that workers strongly preferred eggs during the first two

Table 7. Evolution of larvae-retrieving in 4 colonies
Priority for eggs
°Significant with $P < .05$
°°Significant with $P < .01$
SR: Sum of ranks for larval transport
nl: Number of larvae transported during the 10 first transports

		Colony			
Test		n°59	n°114	n°102	n°67
1st	SR	127	138°°	134°	147°°
	nl	3	3	3	2
		$\bar{x}$ SR = 136,5 $\bar{x}$ nl = 2,75	χ^2 = 14,45	P<.01	
2nd	SR	139°°	127	127	128
	nl	2	3	4	4
		$\bar{x}$ SR = 128,75 $\bar{x}$ nl = 3,25	χ^2 = 7,38	P<.01	
3rd	SR	122	123	121	94
	nl	4	5	6	6
		$\bar{x}$ SR = 115 $\bar{x}$ nl = 5,25	χ^2 = 0,05	non significant	

trials (a mean score of 2.75 transports for larvae during the first 10 transports). The familiarisation which took place during the first test was sufficient to diminish this preference slightly. Since X^2 decreased from 14 to 7 between the first two trials. No preference at all could be detected after 24 hours' familiarisation (X^2 non-significant in 3rd trial). It would be interesting to know if the preference for larvae reappears in the long term. After 48 hours, a score of 73 was obtained (7 larvae in the first 10 transports) which was comparable with the control animals.

One can conclude that early experience of *Lasius* workers has a profound effect on their preference for brood. The effect of larvae deprivation is rapidly reversible, only 48 hours with larvae are necessary to restore normal behavior. It is suggested that this is a fundamental aspect of social behavior which requires no early experience but which is expressed very rapidly once the social environment makes it an advantage to do so.

In the second experiment the choice test was carried out on colonies deprived of larvae until the onset of hibernation (at the end of October). The activity diminished sharply. Sincely only 45 transports towards the nest were recorded in 12 tests (18.75% of the 240 loads presented) and their duration was increased (most often after several hours). The motivation for transporting towards the colony thus disappears in the autumn when workers are deprived of larvae. It remains at a high level, however, in the normal situation (colonies with larvae).

If the transports are examined in detail, it is apparent that larvae are transported, to the detriment of eggs in certain instances. This occurs in colonies where only a limited number of larvae developed (less than 5 in all cases) but it would seem that this is enough to reveal the workers' preference even if the larvae are removed after a few days. Table 8 shows this difference to be highly significant ($P < 0.01$).

In conclusion brood colony transport behavior is linked to a motivation which is low in ants deprived of larvae contact, but only brief contact is necessary for the behavior to be expressed and maintained up to the initiation of hibernation. It has been shown elsewhere that a lack of larvae contact has little influence on brood care behavior. Ants between 15-25 days of age rapidly adopt larvae which they are offered, and after a few days, they feed them normally (Lenoir, 1979).

D - Discussion

1) Brood transport behavior: Brood transport behavior is a motor pattern which is displayed in a stereotyped fashion but which corresponds to

Table 8. Brood-retrieving activity in colonies which reared during several days some larvae and in colonies entirely deprived of larvae.
$X^2 = 24{,}31, P < .01$

		Partial deprivation of larvae	Complete deprivation of larvae
transports	larvae	15	2
	eggs	0	18

different needs. Meudec (1973, b) described it as a reaction to danger, workers carrying the brood to a safe place. It is a reaction to a stress situation. In the test situation described here, transport results from a search for last brood analogous to the mother rat pulling her offspring back in the nest.

In the first situation (emigration), all individuals must face up to an emergency and react independently of their ordinary activity (Meudec and Lenoir, 1981). In the second situation (brood retrieving), the activity is specific to the ants of the outside service. Hinde (1966) has underlined the necessity of describing an item of behavior according to its consequences for, depending on the environment, such a description is vital for complete understanding of the behavior. This is precisely the case here as brood transport may signify various things depending on the conditions under which it is carried out.

2) Polyethism and brood-retrieving: Wilson (1976) carried out a similar experiment using *Pheidole dentata*, which he referred to as a stress imposed on the nest. The brood was scattered into the surroundings and the number of major and minor workers picking up larvae were counted. 96% of this work was performed by minors, although their activity and age was not given.

Walsh and Tschinkel (1974) used a 2-stage test. First the brood was left near the nest entrance and was taken in by the foragers (in accordance with our results). Then the whole colony was alarmed with a current of air to find out if larvae or nymphs were put in the brood chamber. They did not study the division of labor in these experiments. On the other hand, they found out that when the colony is deprived of alimentary protein, pupae were fetched as prey. Therefore would appear to be an interaction between alimentary motivation and motivation to transport brood to the colony.

The brood retrieving test is a means whereby the foragers of the colony may be identified without the need for long observations. The most active transporters are those that exit first, stay the longest in the fore-nest and are also the best food suppliers.

Weir (1958) made similar observations. He placed *Myrmica* workers in the middle of a circle within which larvae had been stuck with paraffin wax. He noted that:

1° The larger the larvae, the more attractive they were.

2° The workers that spent most time in the nest (nurses) were the least sensitive to the presence of the larvae while foragers located them very quickly. Although Weir was surprised by this result, it is in agreement with our findings.

3) Reproducibility of the test: Since the experimental situation was not standardised, it was necessary to check the validity of the test. It is important not to create panic in the colony and care must be taken not to dislodge the queen. The colony must therefore be handled with care. Despite these difficulties the test appears to be sufficiently coherent, judging by the results obtained on more than 50 colonies, to conclude that it is valid. The agreement between foragers and transporters may even attain 100% at the end of hibernation. In colonies containing rather more workers, the test is less efficient: 70-75% for two colonies containing 60-80 workers (3 or 4 trials).

4) Motivation of brood-retrieving: It was shown that this motivation is very strong and that foragers fetch the brood under all circumstances, even if the rest of the colony is inactive. If one excludes cases of extreme hunger, the brood is the preferred stimulus. It is extremely strong since foreign brood may even be retrieved and adopted.

This motivation is still present at hibernation time which occurs normally and spontaneously in the laboratory. In this case colony activity is minimal, few transporters are seen, but brood transport still occurs. The predictive value of the test is thus low ($<20\%$) but this is due to the overall lowering of the activity level prior to hibernation. Transport behavior reappears immediately following the resumption of vernal activity; in the case of the two colonies, larvae were gathered in a test performed 24 hours after the termination of artificial hibernation.

Transport behavior is partly extinguished in ants reared in the absence of brood (paragraph C). Motivation is linked to distance in *Atta cephalotes*. One metre away, the brood is picked up but 8 metres away it is left and even actively rejected (Robinson and Cherret, 1974).

5) The problem of colony odor: The lack of recognition between colonies is exceptional among social insects. this is at least true of *Halictides* for whom workers are interchangeable (Plateaux - Quenu, 1962: *Evylaeus marginatus*; Michener, 1966: *Dialictus versatus*). The phenomenon has also been described in several species of termites and ants where no intraspecific aggression exists: *Macrotermes natalensis* (Grasse, 1959), *Pogonomyrmex* (Whitford, 1976), *Novomessor* (Whitford and al. 1980), *Myrmica americana* (Ayre, 1971), *Monomorium pharaonis* (Sudd, 1957) *Ponera* (Le Masne, 1952). In *Iridomyrmex humilis*, workers travel ceaselessly from one next to another (Markin, 1968) and colonies may combine without any problem (Dechene, 1970). In *Formica* of the *rufa* group, large polycalic colonies have been observed and workers go from one nest to another but the colony can show aggression towards another. For example, Cherix and Gris (1977) have recorded a colony of *F. lugubris* composed of 1,200 nest spread over 70 hectares. In the case of *F. exsecta*, it is thought that there is one territory for the entire polycalic colony (Pisarski, 1972).

Wilson (1971) distinguished three types of societies according to whether strangers are recognized, accepted or rejected.

a)Strangers are immediately accepted but are less well fed until they acquire the colony odor. This was shown for *Formica polyctena* by Lange in 1960. This is probably the case for some of the species cited above.

b)Strangers are examined at length but no attack is made and they are progressively accepted.

c) Strangers are examined, attacked, killed or thrown out of the nest.

The chemical nature of the odor is unknown. No exocrine gland has yet been found which could produce this substance. Food and nest material seem to influence this odor partially. In termites, Verron (1963) identified a substance responsible of interattraction, but it is not colony specific; the odorous substance appears to be a product of breakdown of wood. Verron, (cited above) showed that such insects deprived of food or fed on cellulose lose all attraction for their conspecifics. The nest odor can also be transferred to nest materials (Hangartner and al., 1970; Hubbard, 1974). Michener (1974) demonstrated some outside influences on the smell of bees and bumble-bees likewise Lange (1960) for *F. polyctena*.

Recently, it has been shown that some ant species mark their home range with a territorial pheromone which is colony-specific: *Oecophylla longinoda* (Hölldobler and Wilson, 1977b, 1978), several species of *Myrmica* (Cammaerts and al. 1977, 1978, 1980), *Atta* (Bazire- Benazet and Zylberberg, 1979) and perhaps *Formica sanguinea* (Sulkhanow, 1979). Metcalf and Metcalf (1970) discovered an "anti-pheromone," which obliterates the ants' ability to perceive the normal recognition scent of other workers in the colony so every individual encountered appears to be an intruder.

Genetic differences have been recorded for the species *Lasioglossum* (Bell, 1974); Barrow and al. 1975; Kukuk and al., 1977). Hölldobler and Wilson (1977, a) hypothesized that the queen is the key to the colony's odor and proposed a simple genetic model involving 2 or 3 alleles and a dozen loci. In army ants the queen is effectively essential for the colony odor (Schneirla 1971). Crozier and Dix (1979) proposed two models for the inheritance of the innate components of colony in social Hymenoptera: an Individualistic model and a Gestalt model. They proposed also a general inbreeding test to estimate the number of loci involved in colony odor.

Justsum and al. suggested (1979) that both endogenous (genetic) and exogenous (environmental) factors contribute to colony odor, the latter being the more important in *Acromyrmex*. In the recognition of strange workers, the two factors appear to synergize each other. Kukuk and al. (1977) think that recognition could be based on a larvae learning (a form of imprinting ?). Jaisson (1972-1975) showed that adult *F. polyctena* were sensitive to a species-odor impregnation mechanism for a few days after eclosion. Le Moli and Passetti (1977) reported similar findings for *F. rufa*. Our results show that recognition also exists at the intraspecific level: workers are capable of differentiating between their own brood and foreign brood of the same species, especially in the autumn when the larvae are less attractive. There is an evident disparity between the ready adoption of brood and young workers and the aggression shown by members of different colonies. Glancey et al. (1970); Walsh and Tschinkel (1974); Robinson and Cherrett (1974); Brian (1975), Hölldobler (1977) and Meudec (1979) suggest that the pheromones in question are non-volatile, contact substances found on the larvae cuticle which are attractive to the workers. Hölldobler (1977) has also circumstantial evidence that pupal pheromones are at least in part contained in the exuvial liquid. The pheromones seem to stimulate nurse ants to assist the young during eclosion. The author concludes "This result leads us to the formulation of an other important problem. Ant larvae, pupae and young callows workers can easily be transferred from one colony to another . . . we can hypothesize that in the brood stages the colony odor is masked by the brood-tending pheromones."

Brian (1975) has suggested that the chemicals spread over the cuticle of the larva may act synergistically with other physical characteristics. *Tapinoma* pupae washed in an alcohol/ether mixture are no longer transported (Meudec, 1979). The present results tend to confirm the idea that between-colony recognition is dependent on the state of the brood. It would be interesting to give artificially stained larvae to a colony containing non-colored brood (and vice versa) in order to study the grown of the two groups of larvae nursed by the same ants. It is, in fact, possible that recognition accompanies larval discrimination since in the event of famine, foreign larvae may be killed first while the familiar larvae are preferentially fed. Montagner (1963) showed that wasp larvae from an unfamiliar colony were fed less than those originating from the same colony. Meudec (1978) confirmed for *Tapinoma* that the adoption of homospecific pupae is an easy matter, although certain pupae are excluded initially and are transported last of all by the most active workers. If the colony odor is linked to the queen, then one would expect to see rapid mixing of the two groups of larvae and complete adoption of strangers. It may also be possible that some ants are capable of detecting a foreign odor while others are not. It has often been observed that some workers (specially nurses) will choose brood from their own colony, while others take larvae at random, but this needs to be checked using labeled workers.

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SUMMARY

When foraging ants find some brood during their searches they retrieve it immediately inside the nest where it is placed with the brood of the colony. This particular behavior was studied in the laboratory. Three retrieving tests are necessary to identify 80% of the foragers, which realize more than 98% of whole alimentation of the colony. A retrieving recruitment can be observed which is different from a food recruitment behavior. In a new young colony (during the first autumn) ants are not strictly specialized: 75% of the individuals are able to retrieve more or less brood. Correspondence analysis has confirmed that brood-retrieving behavior is associated with foraging behavior. It was observed that retrieving exists also at the beginning of hibernation when the colony is quite inactive.

In a choice test foragers prefer large larvae and cocoons to small larvae, which are preferred to eggs. Homospecific brood of a different colony is also rapidly carried. In summer all the larvae are very attractive and soon adopted; but the workers learn to recognize larvae after several days. In autumn, when larvae are hibernating, alien brood is differentiated immediately.

Lack of contact with larvae at the onset of imaginal life influences brood-retrieving behavior: the workers prefer eggs instead of larvae but normal

behavior appears after a few days of contact with the larvae. There is no early experience needed for this aspect of social behavior in this species of ants.

RESUME

Le couvain est très attractif pour les ouvrierès, et lorsqu'elles rencontrent des larves ou des cocons hors du nid, elles les ramènent immédiatement à l'intérieur.

Le transport du couvain vers le nid permet de reconnaitre rapidement au moins 80% des pourvoyeuses de la colonie qui réalisent 98% des transports. La motivation du transport vers le nid est très stable, elle se maintient même a l'entrée en hibernation. Les transporteuses les plus actives sont en même temps les pourvoyeuses les plus efficaces et qui séjournent le plus longtemps dans l'avant-nid. Les ouvrières préfèrent les grosses larves et cocons aux petites larves, et celles-ci sont preferées aux oeufs qui sont parfois negligés. Le couvain étranger (homospecifique) est transporté rapidement et adopté, mais en situation de competition le couvain de la colonie d'origine est transporté prioritairement, surtout en fin de saison lorsque les larves sont moins attractives.

La privation de contacts larvaires influence les préférences envers le couvain, surtout a l'entrée en hibernation, mais le comportement normal est restauré très rapidement au bout de 48h. de familiarisation aux larves. C'est un aspect du comportement social qui ne nécessite pas d'experience précoce.

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