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FEEDING BEHAVIOUR IN YOUNG SOCIETIES OF THE ANT *TAPINOMA ERRATICUM* L.: TROPHALLAXIS AND POLYETHISM

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SUMMARY

The study of alimentary behaviour in newly founded societies of ants *Tapinoma erraticum* (Dolichoderinae) with marks on the gaster enabled us to classify the individuals in terms of foraging and brood care. There are 3 different groups: permanent foragers (foragers in more than 80 % observations), intermittent foragers (between 20 to 80 %) and nurses (less than 20 %). The behaviour of ants changes with age: young ants are nurses at first, then they are intermittent foragers, and permanent foragers at last. Ants less than one month old are called *young* (under laboratory conditions): 65 % of them are nurses, some are intermittent foragers (35 %). Ants more than one month old are called *old*: 60 % are intermittent foragers, 30 % permanent foragers and 10 % only nurses. Young workers become nurses very quickly (in a few days) but they are not active donors to other workers. After one month most of them become members of a pool of unemployed ants able to forage and give food to the queen or larvae. Most of the foraging is done by permanent foragers, older workers. Individual development is very variable, according to social pressure, if there are not enough old foragers, young ants become foragers. This phenomenon can be reversible.

RESUME

Le comportement alimentaire dans les jeunes sociétés de la Fourmi Tapinoma erraticum **L.: trophallaxie et palyéthisme**

L'observation des jeunes sociétés de Fourmis *Tapinoma erraticum* (Dolichoderinae) a permis de classer les individus en fonction de leur activité dans l'approvisionnement du nid, celui-ci est effectué par des ouvrières spécialisées: les pourvoyeuses. On reconnaît

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3 catégories d'ouvrières : *les pourvoyeuses permanentes ;* elles sont pourvoyeuses dans plus de 80 % des observations et ne sont jamais nourrices, les *pourvoyeuses intermittentes* (de 20 % à 80 %) qui peuvent être simultanément pourvoyeuses et nourrices de larves, enfin les nourrices strictes (moins de 20 % des observations) qui s'occupent presque exclusivement du couvain.

Le comportement est en relation avec l'âge : les ouvrières sont d'abord nourrices, ensuite pourvoyeuses intermédiaires et enfin pourvoyeuses permanentes. Les fourmis âgées de moins d'un mois sont en grande majorité nourrices (65 %), quelques-unes sont pourvoyeuses intermittentes (35 %). Parmi les ouvrières âgées de plus d'un mois 60 % sont pourvoyeuses intermittentes, 30 % pourvoyeuses permanentes et 10 % restent nourrices. Les jeunes ouvrières deviennent en quelques jours de bonnes nourrices et soignent activement les larves alors qu'elles sont très mauvaises donneuses envers les autres ouvrières. A partir d'un mois, la majeure partie des ouvrières entre dans un pool d'individus disponibles selon les besoins de la colonie, ils sont pourvoyeurs mais peuvent aussi nourrir les larves ou la reine. La plus grande partie de l'approvisionnement est assurée par les pourvoyeuses permanentes qui sont de vieilles ouvrières et peuvent présenter une préférence alimentaire marquée vers des aliments de type sucré ou protéique L'évolution individuelle est très variable, elle peut être influencée par la pression sociale : s'il manque des pourvoyeuses âgées et c'est le cas lorsque le nombre de jeunes ouvrières est supérieur à celui des ouvrières âgées, les jeunes de moins d'un mois peuvent devenir momentanément pourvoyeuses.

INTRODUCTION

Division of labour among ants has been known for a very long time. Though studies of the individual behaviour of ants are very numerous (WILSON review 1971, p. 163) no systematic study has yet been done on newly founded colonies or *fondations.* In the species studied, dissemination occurs when the swarming female (mated queen) looks for a hole to lay her first eggs in and then takes care of them alone. At the end of the first season there are a few workers to help the queen to tend the brood and search for food for the young colony. The following year there are more workers but they can be still counted in tens, and their number will seldom reach a hundred. Workers are always small. The colony does not produce alates. We have studied the structure of these embryonic societies by marking individuals. Since it is not easy to follow simultaneously many individuals the groups studied were of between 10 and 30 ants.

In this paper we discuss observations made on the ant *Tapinoma erraticum* L. The biology of this species has been described by Meudec (1973 a).

MATERIAL AND METHODS

Ants were reared in glass tubes, 30 centimeters long, with interior diameter of 1 cm. One end of the tube was closed by cotton-wool and at the other end there was a water supply (LENOIR 1973). Ants were fed on honey and on pieces of *Tenebrio* larvae.

Each worker was marked using a technique developed in the laboratory : a tiny nickel plate bearing a figure or a number is stuck to the gaster (VERRON and BARREAU 1974). During the operation the ants were anaesthetized by CO_2. For studying feeding behaviour the groups were starved for a period of 24 or 48 hours. If this period of starvation is too long, workers begin to eat larvae, or give eggs and young larvae to older larvae, which could invalidates the results of food recruitment experiments.

The experiment consisted simply in observing, using a binocular microscope, the exchanges of regurgitated food (*trophallaxis*) following the introduction of food at the end of the tube (a larva of *Tenebrio* and a drop of honey). All behaviour related to foraging and food-sharing has been noted ; exchanges between foragers, other workers larvae, and the queen. Each trophallaxis was timed. Most of the time, observations did not last more than half an hour, after which time, activity considerably diminished if the need for food was not very strong.

The results are partly presented as diagrams called " *sociograms* ". Trophallaxie is shown as arrows the head pointing toward the ant which receives food. This time taken by foragers to feed on honey or *Tenebrio* is also represented by an arrow whose width thickness represents the length of time sharing lasted. A sociogram is the image of the colony behaviour at one time ; it is a picture of a group which keeps on changing. Each group is unique at a precise time. However some comparisons may be carried out to understand the different influences contributing to the structure of the society and the development of individuals.

DESCRIPTION OF THE DIFFERENT COLONIES

1 — Colony BX (fig. 1)

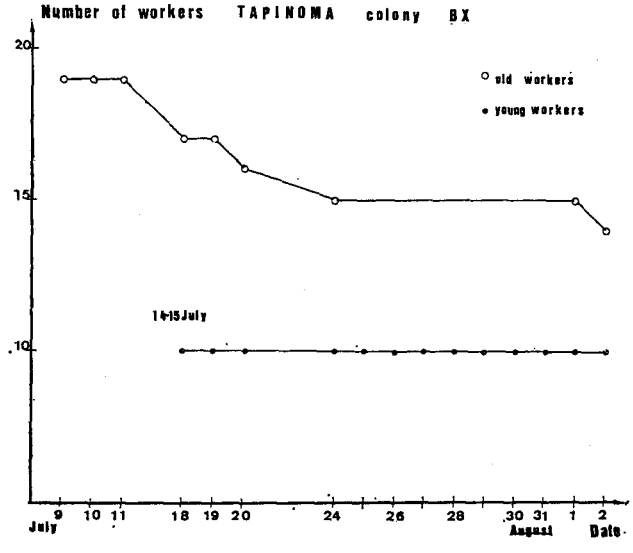

Fig. 1. — Number of old and young workers in colony BX. On each date there was an observation of half an hour. Young workers hatched on July 14-15th.

Fig. 1. — Nombre de vieilles ouvrières et de jeunes ouvrières dans la colonie BX. A chaque jour correspond une observation de 30 mn. Les jeunes ouvrières sont nées le 14-15 juillet.

This colony consisted, at the beginning, of 2 queens and 19 " older " workers. An " older " worker is any individual whose age we do not know, but which is dark coloured and is at least 25 to 30 days old when the experiment started. Young workers, on the other hand, are newly hatched ants, and are less than 30 days old when the experiment ends. We made premiminary observations every day during 3 days. As there were many pupae 10 workers were born on July 14-15th. The colony with young workers was observed 13 times in 2 series : on July 18-19-20th and then every day between July 24th and August 2nd. At the end of the experiment, young workers were just about 15 days old. The number of large larvae had increased by a factor of two (from 25 to 51), while the number of young larvae and eggs has decreased (220 to 170) as might be expected when starvation lasts for a long time. Periodic egg production by the queen may also play a role. No food had been given during the experimental period, except when observations were being made.

2 — Colony CB (fig. 2)

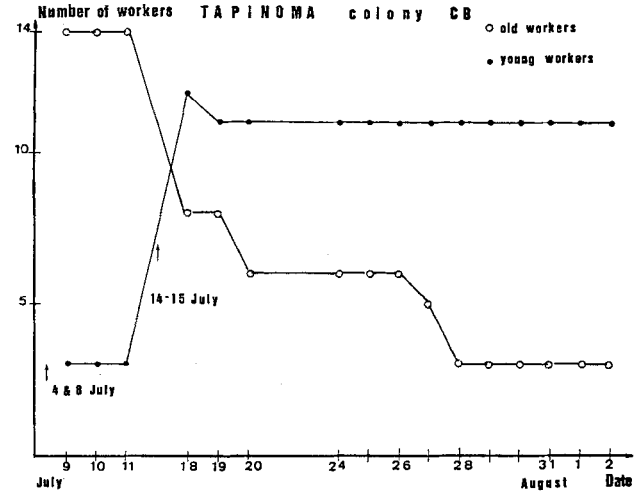

Fig. 2. — Number of old and young workers in colony CB. On each date there was an observation of half an hour. 3 young workers hatched between July 4th and 8th, 9 others on July 14-15th. 6 old workers were drawn back down between the 15th and 18th and many others died.

Fig. 2. — Nombre de vieilles ouvrières et de jeunes ouvrières dans la colonie CB. A chaque jour correspond une observation de 30 mn. 3 jeunes ouvrières sont nées entre le 4 et le 8 juillet, les 9 autres entre le 14 et le 15 juillet. 6 vieilles ouvrières ont été retirées entre le 15 et le 18, et la plupart des autres sont mortes.

This colony was observed during the same period as colony BX. It included one queen, 14 old workers and 3 young workers, 5 days old. Unfortunately most of the old workers died during the course of the experiment (6 were removed between 15 and 18th and the others died later). There were no more than 3 old workers left at the end. The brood had not changed very much : 17 to 25 large larvae. The same data were found for young larvae and eggs in colonies BX and CB (220 to 170 for CB).

The two colonies were collected in June 1973, before the experiment.

3 — Colonies T II to T VI

These five colonies were studied at the end of their hibernation period in the laboratory in April. Therefore, at the beginning, there were only older workers, born either during the summer time or the preceding autumn. Six observations were made,

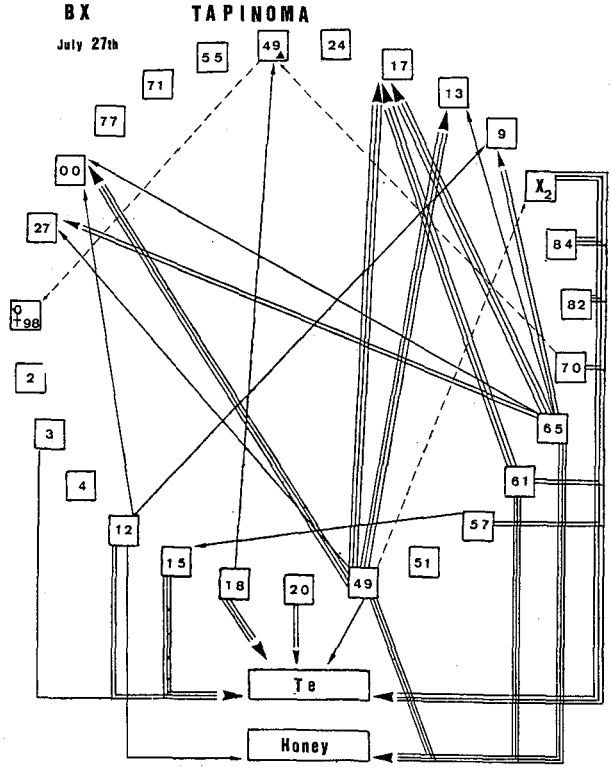

Fig. 3. — *Sociogram* of colony BX on July 27th. Queen is marked n° 98. Trophallaxis are represented like arrows whose head points toward receiving ant or larvae. Their thickeness is in relation with the duration of exchange. The time passed by foragers to feed on honey or *Tenebrio* is also represented by an arrow.

0 to 50 sec. .....
50 to 100 sec. ———
100 to 200 sec. ═══
More than 200 sec. ═══

Fig. 3. — Sociogramme de la colonie BX le 27 juillet. La reine porte le n° 98. Les trophallaxies sont représentées par des flèches dont la pointe est dirigée vers la fourmi ou les larves receveuses. Leur épaisseur est proportionnelle à la durée de l'échange. Le temps passé dans le milieu extérieur sur le miel ou le *Tenebrio* est aussi représenté par une flèche.

0 à 50 sec. .....
50 à 100 sec. ———
100 à 200 sec. ═══
> 200 sec. ═══

at the rate of one a week, after a period of starvation of 48 hours, at the time of the emergence of the first workers born from the wintering brood. This was in May-June 1974. Each colony had only one queen (in colony T II the queen died during the third week). All 5 colonies had a small brood, never more than 50 larvae.

The death rate was very high among older workers during the six weeks observation, while there were almost no deaths among young workers. The rate of death varies between 82 % for T V and 27 % for T III. That is an average of 70 % for old hibernating workers and 8,5 % for young workers 3 or 4 weeks old.

Typical behaviours

The observed behaviours have been described in *Lasius niger* (LENOIR 1974) and are illustrated by figures 3 and 4.

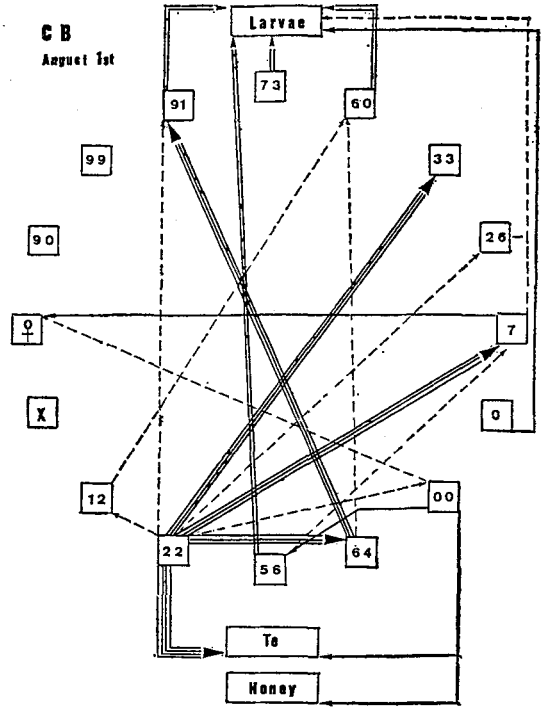

Fig. 4. — Sociogram of colony CB on August 1st.
(see symbols on fig. 3)

Fig. 4. — Sociogramme de la colonie CB le 1er août.
(voir symboles fig. 3)

Foragers search for food at the end of the tube and return to the group of sedentary ants to give them the liquids stored in their crops.

It is interesting to note that some foragers show personal preferences either for insects or for honey. They feed on honey or on *Tenebrio* more than 70 % of observations. The proportion of foragers showing a marked alimentary preference is variable according

to the different colonies 75 % for BX, 50 % for CB, 10 to 30 % for T II - T VI. This shows that there might be a *specialisation in the alimentary behaviour of some foragers.* This specialisation should be studied in the field or in an artificial nest with a larger colony.

Nurses feed larvae. They receive food from foragers or receivers which act then as an intermediary.

Some workers are inactives when the sharing of food is concerned.

RESULTS

1 — Individual development

At the end of the observations ants were classified according to the % number of times they showed a foraging behaviour.

— More than 80 % of the tests : *Permanent Foragers* PF

— From 20 to 80 % : *Intermittent Foragers* IF

— Under 20 % : *Nurses* N

1 - Permanent Foragers PF

Permanent foragers may rest passively, but they stand near the entrance or outside the nest. It is normally a permanent forager which discovers the food source, comes back to the nest and recruits nestmates with a recruitment-display. It may then become an Inactive. Half these ants are *never* receivers. The others are rarely so. The ratio of time spent feeding (regurgitating) / receiving (F/R) is always more than 5, usually as large as 50 and may be infinite when no receiving occurs (Table I). They do not tend the brood and very seldom lick larvae or carry them.

These ants are not very numerous : 28 % old workers in CB-BX, and 31 % wintering workers in T II - VI (Table II A). They are always old. Only one example of a young workers behaving like a permanent forager (twice successive times after emergence, i.e. 100 % of th two observations for this ant) has been found, but it was not active and did not share food (Table II B *). In our colonies PF represented 10 to 15 % of the worker population.

2 - Intermittent Foragers IF

These are workers which can forage if necessary, for example, to feed young workers or brood. They can be characterised by an intermediate % number of foraging behaviour : 20 to 80 % of the observations. They are numerous in the colonies : 57 % of hibernating ants in T II - VI, 67 % of old workers in CB-BX (Table II A). They represented 47 % of the total population of our colonies (Table II B).

Those IF are what we described as " disposable " (available) in a preliminary work with *Lasius* (1974). They are either more inclined to forage outside or more inclined to rest inside tending the brood, as necessary. They may be classified in 2 categories :

Table I. — Summary of characteristics of individuals in CB - BX colonies during 10 days observation samples. Activities connected with feeding larvae are not shown.

Tableau I. — Résumé des caractéristiques individuelles des ouvrières des colonies CB et BX, établies après 10 jours d'observations. Les activités associées à l'élevage de larves ne sont pas quantifiées.

Colony	Worker n°	% foraging	F	R	F/R
PERMANENT FORAGERS					
CB	22	100	9 530	0	
	00	100	3 920	440	9
BX	12	100	5 830	0	
	65	100	7 540	0	
	57	90	1 210	150	8
INTERMITTENT FORAGERS					
CB	64	30	880	770	1.1
	12*	40	200	210	0.95
	56*	20	530	1 350	0.4
	60*	20	140	2 060	0.06
BX	3	50	60	840	0.07
	4	70	440	250	1.8
	15	30	0	1 400	0
	18	30	810	1 410	0.57
	20	40	200	1 000	0.2
	49	30	1 450	560	2.6
	51	60	70	30	2.3
	61	50	390	580	0.7
	70	50	310	380	0.8
	82	70	880	380	2.3
	84	40	200	610	0.3
NURSES					
CB	0*	10	240	3 110	0.07
	7*	0	40	1 880	0.02
	26*	0	20	1 160	0.01
	33*	10	80	3 110	0.02
	73*	0	490	2 110	0.2
	91*	0	0	1 140	0
	99*	0	50	1 440	0.03
	90*	0	90	1 140	0
BX	X2	10	0	800	0
	9*	0	0	860	0
	13*	0	30	1 740	0.02
	17*	0	0	1 750	0
	24*	0	0	1 500	0
	27*	0	760	1 030	0.7
	49*	0	10	250	0.004
	55*	0	0	310	0
	71*	0	0	970	0
	77*	0	0	1 270	0
	00*	0	0	1 610	0

% foraging: % observations where the worker is forager.
F: total time feeding other worker or queen (seconds).
R: total time receiving.
F/R: ratio Feeding/Receiving.
*: young worker.

% foraging: % des observations où l'ouvrière est pourvoyeuse.
F: temps total passé à nourrir d'autres ouvrières ou la reine (secondes).
R: temps total passé à recevoir de la nourriture.
F/R: rapport activité de donneuse / activité de receveuse.
*: jeune ouvrière.

a - *Strongly inclined to foraging* (50 to 80 % observations) (Table I)

These are ants which are observed mostly outside the nest. They may also be receivers, the ratio feeding/receiving is less than one (they receive more than they regurgite). They never or seldom lick brood. CB-BX workers 3, 4, 51, 61, 70 and 82 were classified in this group (Table I).

b - *Not inclined to foraging :* these are foragers in less than 50 % observations. Very often they leave the nest to forage only towards the end of the period of observation. Their activity is very variable : some are good donors. F/R is in 7 cases out 9 (80 %) less than one for this group of workers.

The work efficiency of foragers, measured by the total time during which regurgitation occurs clearly shows that permanent foragers are much more active than intermittent foragers.

3 - Nurses

These practically always remain inside the nest, near the queen and brood, or stand on it. They lick larvae and eggs, they also move them and collect them in piles. Nurses are very active receivers. They are rarely foragers (see table I n° 0, 33 and X_2 for 10 %) and if they are, they regurgitate very little food. Thus F/R is always smaller than 1, and very often 0 or near (Table I). The nurses sometimes fed larvae during the observation period. This behaviour takes place after a short period of antennal stroking. During regurgitation the mandibles of the nurse are wide open around the head of the larvae. If the larvae are small, nurses grip them between their forelegs to put the head of the larvae between their mandibles.

4 - Development of behaviour depending on the age of the ant

Young ants, after hatching from the pupae, are generally receivers only, and in a few days they are able to feed brood. They become nurses and stand on brood as has been described above. They are able to leave the nest at 4-5 days of age and they become foragers for one or two days. When they are one week old they may become intermittent foragers, for example 12, 56 and 60 in CB (Table I). This behaviour shows a great plasticity and demonstrates that the ethological groups I have determined (permanent foragers, intermittent foragers and nurses) provide a convenient classification, that is not an absolute one, where all intermediaries exist.

Among the older workers very little difference can be noticed between the wintering workers and the workers whose age is unknown but who are definitely more than 25 days old (Table II A). We can thus consider that a one month old ant is *already old in the laboratory environment.* Among these individuals, about 30 % are permanent foragers, 60 to 70 % intermittent foragers and 5 to 10 % nurses. It must be added that old nurses are very bad nurses as they do nothing, most of the time, and very seldom regurgigate

Table II. — Frequency of various ethological groups of workers in relation with age.

Tableau II. — Fréquence des divers groupes éthologiques en relation avec l'âge des ouvrières.

A — Ants of unknown age (more than 25 days old at the beginning of the experience) and wintering ants.
x^2 = 0.008 not significant (when grouping IF and N)
x^2 1.d.l., .05 = 3,84)

A — Fourmis d'âge inconnu (plus de 25 jours au début de l'expérience) et fourmis hivernantes.
x^2 = 0,008 non significatif (en regroupant N et IF)

		PF	IF	N	Total
" Old " workers > 25 days	Number	5	12	1	18
	%	27.8 %	66.7 %	5.5 %	100 %
Wintering workers	Number	9	17	3	29
	%	31 %	56.8 %	10 %	100 %
	Mean	29.8 %	61.7 %	8.5 %	

B — Both old and wintering ants compared with young ants.
x^2 = 30.157 P < .001 (when grouping PF and IF)
(x^2 1.d.l., .001 = 10.83)
* Young worker outside the nest but completly inactive.
x^2 are calculated with correction for continuity of Yates (2 × 2 contingency tables).

B — Comparaison entre fourmis âgées ou hivernantes avec jeunes.
x^2 = 30,157 P < .001 (en regroupant PF et IF)
* Jeune ouvrière à l'extérieur du nid, mais complètement inactive.
Les x^2 sont calculés avec la correction de continuité de Yates (tableau de contingence 2 × 2).

		PF	IF	N	Total
Old (> 25 days) and wintering workers	Number	14	29	4	47
	%	29.8 %	61.7 %	8.5 %	100 %
Young workers (< 30 days)	Number	1*	21	37	59
	%	1.7 %	35.6 %	62.7 %	100 %
	Mean	14.1 %	47.2 %	38.7 %	

PF : Permanent forager
IF : Intermittent forager
N : Nurse

PF : Pourvoyeuse permanente
IF : Pourvoyeuse intermittente
N : Nourrice

to larvae or care for them ; for e.g. X_2 in colony BX (Table I) or 76 in T V. This last ant died during the 4th week.

Among young workers the results are quite different. 65 % are nurses and 35 % intermittent foragers (Table II B). The difference between young and old workers is very significant ($P < 0.001$ with χ_2). Here we see a phenomenon well known among ants : younger ants are nurses at first and then they become foragers. A problem attracted our attention : are the permanent foragers the oldest workers ? At present we cannot answer this question because some individuals might become permanent foragers at once or remain intermittent only for a short while, according to the social environment.

2 — Influence of the hatching of young workers

The hatching of young workers creates new needs for food in the colony since these new ants are active receivers. If the food supply is not sufficient they may leave the group to search for food. The total trophallactic activity of the colony BX was low on July 9th, 10th and 11th in the absence of young workers. It increased greatly after the hatching of the young and remained at a high level, more than 4 or 5 times the starting level.

Figure 5 represents on the abcissa the number of young workers and on the ordinate the trophallactic activity of the whole colony. The graph clearly shows a positive linear correlation ($r = 0.770$, $P < .01$).

Table III indicates the levels of trophallactic activity (measured in seconds) for either foragers or receivers for one observation. We have reported the durations of regurgitation for foragers, and receiving for receivers. The animals are classified in groups : feeble activity (from 0 to 59 sec), medium activity (from 60 to 199), high activity (from 200 to 599 sec) and very intense activity (600 sec that is more than 10 minutes).
Results are presented as a function of the ratio Y/0 : number of Young workers/number of Old workers.

— *Y/0 = 0 :* There are no young workers and with moderate starvation (24 or 48 h) the trophallactic activity is generally very low.

— *Y/0 < 1 :* The number of young workers is smaller than the number of old workers. The activity of the colony is greater but ranks at a medium level (between 800 to 1 600 seconds, and one at 4 000). The young workers are not foragers.

If we look at table III A, we can see that the trophallactic activity of the young is very high. They are active receivers, but there is a great variability between individuals : 27 % show a feeble activity, on the contrary 53,9 % (38,5 % + 15,4 %) show a high or very intense activity. Foraging is done by old workers (Table 3 B, 2nd line).

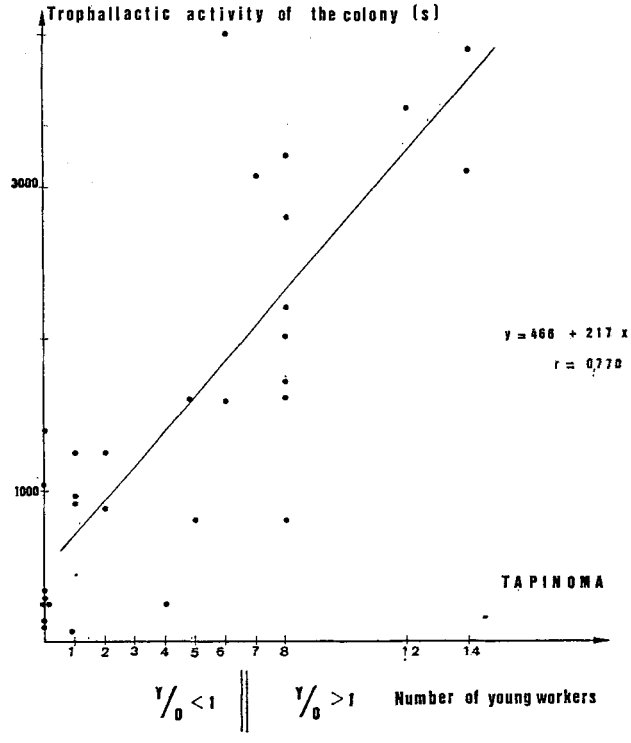

Fig. 5. — Correlation between total trophallactic activity of the various colonies and the number of young workers.
r = 0.770 is significant with $P < 0.01$.

Fig. 5. — Corrélation entre l'activité trophallactique totale des colonies et le nombre des jeunes ouvrières.
r = 0.770 significatif avec $P < 0.01$.

— *Y/0 > 1 :* Young workers are more numerous than old workers and the activity of the colony is much higher. In 70 % of cases the total activity of the colony is superior to 2 000 seconds (25 minutes of trophallaxis for 30 minutes of observation, which is possible because there are simultaneous exchanges). We have observed that in this situation young workers become foragers. Young workers are sometimes only 4-5 days old, more often they are 10 or 15 days. The young workers which remain receivers appear more active than in the case $Y/0 < 1$ (Table III A) : 27 % are very active as against only 15 % when there are no young foragers but the χ_2 obtained is 0.358 which is not significant. *Foraging is thus the work of both young and old workers.* The latter are much more efficient since in 24 observations 40 % old workers are very intense donors when only 8 % young workers are (Table III B, lines 3 and 4 - χ_2 significant with $P < 0.02$).

Table III. — Trophallactic activity (in seconds) of the individuals of colonies T II - VI, for *one* observation (half an hour).
Ants are foragers (feeding) or receivers.
3 A : time during which young workers are receiving food from foragers.
$x^2 = 0.358$, 1 d.l. $P > .90$
3 B : time during which young or old workers are giving food to receivers. There are 3 situations in relaiton with the ration Y/O (young / old workers) : Y/O = 0 (only old workers) Y/O < 1 less young than old, and Y/O > 1 more young than old workers.
x^2 between old workers = 28.957, 3 d.l., $P < .001$
x^2 between young and old workers when Y/O > 1 = 6.402, 1 d.l., $P < .02$
x^2 are calculated with two groups : feeble + medium and high + very intense activity (correction for continuity of Yates has been used for 2×2 contingency tables).

Tableau III. — Activité trophallactique (en secondes) des individus des colonies T II à T VI, pour une observation de 30 mn. Les fourmis sont donneuses ou receveuses.
3 A : Activité de receveuse des jeunes ouvrières nourries par les pourvoyeuses.
$x^2 = 0{,}358$ P > .90
3 B : Activité de donneuse des pourvoyeuses jeunes ou âgées suivant le rapport Y/O (nombre de jeunes ouvrières / nombre d'ouvrières âgées).
Y/O = 0 : uniquement des vieilles ouvrières
Y/O < 1 : moins de jeunes ouvrières que de vieilles
Y/O > 1 : plus de jeunes ouvrières que de vieilles
x^2 entre vieilles ouvrières = 28,957 P < .001
x^2 entre jeunes et vieilles quand Y/O > 1 = 6,402 P < .02
Les x^2 sont calculés en regroupant faible + moyenne activité et forte + très forte activité et en utilisant la correction de continuité de Yates pour les tableaux de contingence 2×2.

Workers		Situation	0-59 sec. feeble	60-199 sec. medium	200-599 sec. high	> 600 sec. very intense	Total	
3 A		Y/O < 1	7	5	10	4	26	Number
			27 %	19.2 %	38.5 %	15.4 %	100 %	%
Young receivers		Y/O > 1	18	2	20	15	55	Number
			32.7 %	3.6 %	36.4 %	27.2 %	100 %	%
3 B	old	Y/O = 0	41	7	2	2	52	Number
			78.8 %	13.5 %	3.8 %	3.8 %	100 %	%
Foragers	old	Y/O < 1	27	10	12	4	53	Number
			50.9 %	18.9 %	22.6 %	7.5 %	100 %	%
(giving)	young	Y/O > 1	27	6	11	4	48	Number
			56.25%	12.5 %	22.9 %	8.3 %	100 %	%
	old		9	3	7	13	32	Number
			28.1 %	9.4 %	21.9 %	40.6 %	100 %	%

It is possible to conclude that when Y/0 < 1 there are no *young foragers.* We have noted only one exception during 26 observations (4 %). On the otherhand, when Y/0 > 1, *young workers become foragers* after a one day starvation period (no exception during 13 observations). This phenomenon

is probably temporary and reversible : young workers which have left the nest to forage become nurses again after a few days (as in CB). The foraging behaviour is influenced by social pressures : when there are many workers or very few old foragers there is a change in the behaviour of young individuals. This phenomenon is a *social regulation of behaviour.*

3 — Effect of the forager mortality

In the colony BX, the food requirements were very high due to the presence of young workers which were very active receivers in the first days after emergence. The needs were easily supplied by the pool of old intermittent foragers which efficiently furnished the nest. The total number of foragers passed from 4 to a maximum of 17 (all old workers except one, and 2 young workers). This phenomenon is shown on figure 6 which

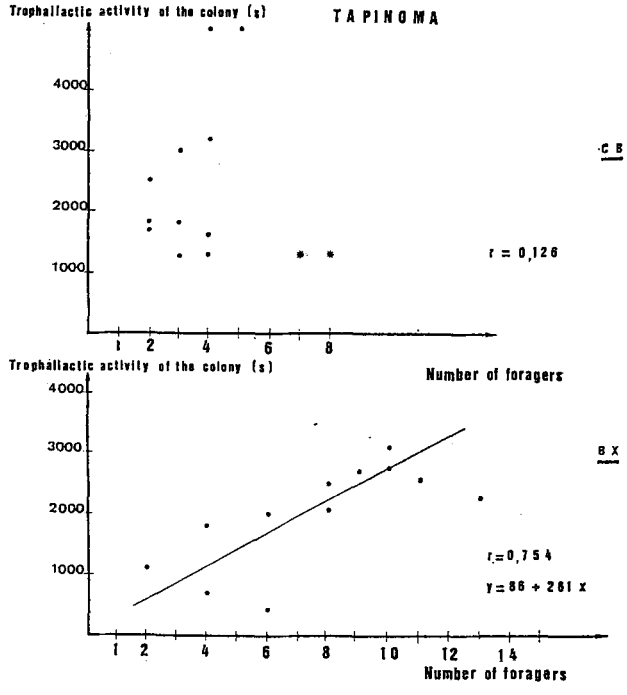

Fig. 6. — Correlation between total trophallactic activity and number of foragers in colonies CB and BX.
CB : r no significant.
BX : r significant with $P < 0.01$.
* young workers forage (see text).

Fig. 6. — Corrélation entre l'activité trophallactique totale et le nombre de pourvoyeuses dans les colonies CB et BX.
CB : r non significatif.
BX : $r = 0.754$ significatif avec $P < 0.01$.
* : jeunes ouvrières pourvoyeuses (voir texte).

represents the total trophallactic activity of the colony (in seconds) as a function on the number of foragers. There is a very significant correlation ($r = 0.754$, $P < .01$).

For the colony CB we must go back to Figure 2 : most of the old foragers died after a few days. There was one permanent forager which died when young workers emerged from the pupae. 6 old workers were removed on July 18th, 4 others in the following days. Individual 00 and 4 become permanent foragers and 22 soon joined them. The linear function between trophallactic activity and foraging was not found again in colony CB ($r = 0.126$). It was even observed that during the 10th day, 2 young workers went foraging and 5 on the 18 th day (fig. 6). 2 young workers only went out on the 19th day and then the phenomenon stopped (see paragraph on Y/0). It was concluded that *only old workers can quickly become permanent foragers.* Young workers are able to help temporarely in the search for food but cannot immediatly take the place of permanent foragers if they disappear.

4 — Discussion and conclusions

1 - Age polyethism in Tapinoma

The structure of the society and division of labour corresponds to known models. Differences in behaviour depend on the age of the ants : young ants are nurses and older ones foragers.

— Younger workers usually remain motionless on the brood, near the queen. When their pigmentation is completed (in two or three days) they become very active receivers and feed larvae. When they are 10-15 days old they are good nurses. The maturation of the donor behaviour in relation with other workers is very slow and even if they become foragers prematurely their activity is always lower than the activity of older foragers. This fact suggests that regurgitation is not the same for a worker as for a larvae younger workers are good donors to larvae and bad donors to other workers.

One reason could be that in young workers the glands (esp. postpharyngeal glands) are still active and there might be transferred more glandular secretions rather than regurgitated crop content. NAARMAN (1963) on *Formica* and MARKIN (1970) on *Iridomyrmex humilis* have shown that substantial amounts of glandular secretion are transferred with regurgitated materials to queens and small larvae. BUSCHINGER and KLOFT (1973) could find out similar situations in colonies of *Monomorium pharaonis* (L.). Thus young workers tending the queen (s) as " Hofstaat " serve like a screen against poisenous baits transferred by regurgitation of crop content.

— *From the 3rd or 4th week* (or earlier according to social pressure as will be discussed later) all the workers form a *pool* of available individuals doing

nothing for most of the time. They are able to feed the brood, to forage or both. We have called these workers intermittent foragers. This phenomenon has already been observed in *Lasius niger* (LENOIR 1974) and SUDD (1967 p. 161) mentions this point. It is not known if these workers " doing nothing " are also found in the field where they might be doing tasks impossible in an artificial nest. Sudd thinks that this is a general phenomenon as it is also ordinarily observed in bee hives.

— After that some individuals become permanent foragers. They are probably the oldest ants (particulary overwintering ones). These workers are not numerous but they are very busy and supply most of the colony food. They may specialise in sweet diet (honey) which they quickly share whereas temporary foragers often prefer a meat diet (*Tenebrio*) keeping the haemolymph in store in their crop. SCHNEIDER (1972) pointed out that in *Formica polyctena* large quantities of food taken up by some individuals may remain in the crop, unregurgitated. This kind of specialization has already been studied in this species : KILL (1934) has observed that some individuals are hunters and others collect honeydew. OTTO (1958) discovered that honeydew collectors are smaller than hunters. HORSTMANN (1973) confirmed the existence of these specialists in the foraging area. This is also found in *Camponotus* where workers collecting nectar are larger than honeydew collectors (GOTWALD 1968). In our experimental foundations, workers are all small individuals, and specialization might be linked with age only (but the size of workers has not been measured). It is difficult to compare age polyethism in *Tapinoma erraticum* with the results of OTTO (1958) in *Formica polyctena* as we only observed small colonies where the passage from one task to another is certainly very easy. The temperature of our nests (25°C) probably accelerated the rate of development.

Otto has pointed out that the passage from inside the nest to outside the nest is affected after the 45th day. In our tube nests there is no definite borde line between those 2 regions, *Tapinoma* workers often stay near the place where the queen and the brood are. We have chosen the time when the workers begin to come outside the brood area and explore the extremity of the tube where food is given ; they become intermittent foragers, and can be compared with *Formica* workers doing outside tasks.

In the genus *Myrmica* 3 species have been studied : *Myrmica scabrinodis* and *Myrmica ruginodis* (WEIR 1958 a, b) and *Myrmica rubra* (BRIAN 1974). In *Myrmica* it has been known for a long time that pale young workers are nurses and that they change into foragers as they darken and age (EHRHARDT 1931). Weir recognised three worker jobs : nurses, domestics and foragers. The % time spent by workers on brood, near brood and away from brood, the brood rearing efficiency and nest-building capacities were observed. Brian has classified workers, on the basis of time spent on/off brood into nurses ($\geqslant 2$), foragers ($\leqslant 0.5$) and intermediates ($< 2, > 0.5$). Activities

connected with brood are : standing on brood, grooming and feeding small, worker-biaised larvae, and chewing prey. Activities connected with foraging are standing away from brood, exploring and collecting food. Pale workers usually nurse and dark one usually forage or behave as intermediates, but there are exceptions. Brian thinks that intermediates seem to correspond with domestic. Weir regarded the domestics as a mobile reserve of foragers. It is interesting to see that our conclusions are similar, for two other species *Lasius niger* (LENOIR 1974), and *Tapinoma erraticum* in this study. We propose to call domestics or intermediates, *intermittent foragers* because they represent a pool of available individuals.

2 - Individual development and interindividual variation

OTTO (1958) has already pointed out that some *Formica polyctena* workers pass to the outside tasks without feeding the brood, when some others on the contrary did not leave the nest before they were 80 days old. Such an interindividual variation has also been observed in this studies, both for the activity and for individual development.

The activity of ants of the same age or of the same class of age when it is not known exactly is very variable. Some young workers tend the larvae (feed, lick and displace) when others rarely or never do so and just stay on the brood, they are all called nurses in as much as they do not come out of the nest.

Variability is also very important between workers for trophallactic activity as has been shown in Table III. The heterogeneity of response between individuals of a group has recently been demonstrated in the olfactive interattraction (VERRON 1973) and locomotor activity (VERRON 1974) for *Lasius niger,* and in the carrying brood (MEUDEC 1973 b) for *Tapinoma erraticum.*

Individual development is linked to age, but, in a group of workers of the same age, some come outside the nest early, others are nurses for a longer time. For example in colony CB, 2 workers hatched on July 4th, n° 12 become intermittent forager on 18th and n° 56 only on 27th (23 days old). Of the 9 workers hatched on July 14-15th, 3 become intermittent foragers on 27th and 6 were still nurses on August 2nd. In colony T IV 3 workers, only 4-5 days old, become intermittent foragers. The duration of the nursing stage is very variable, from 4-5 days to 2-3 weeks in general, and sometimes more (under laboratory conditions). This variability is influenced by social regulation.

3 - Social regulation

This is very important, even in a small colony. It occurs when the foragers die or when there are not enough older workers to feed the colony by the early development of foraging and donor behaviour in young

ants. When the ratio Young/Old workers is more than one, some young workers may leave the nest and become intermittent foragers (colonies T II - VI). This change of behaviour is sometimes reversible : after a few days or one day only, young workers ceased their task and become nurses again when enough food was provided (colonies CB-BX).

The acceleration of the development of the behaviour of young worker has already been reported when there are no old workers by EHRHARDT (1931) in *Manica rubida,* DOBRZANSKA (1959) in *Formica sanguinea,* CHAUVIN (1969) in *Formica polyctena,* and we have often observed it in *Lasius niger* (work in progress). Groups of young workers of the same age very quickly organise themselves into nurses and foragers. The presence of a few older workers is sufficient to prevent the modification of behaviour or at least to limit it, as we see in these studies. This is perhaps connected with the influence of older workers on the development of ovaries of young workers. OTTO (1958) established in *Formica polyctena* that ovaries come to maturity from the 10th to the 30th day and then degenerate, when the ants leave the nest. Workers which were kept without older ones did not develope ripe ovaries. The presence of older workers influences the ovarian activity of the young which become foragers when the ovaries degenerate. If there are no older workers there is no ovarian development and some workers might become foragers directly.

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