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# FORAGING RECRUITMENT IN *LEPTOTHORAX UNIFASCIATUS* : THE INFLUENCE OF FORAGING AREA FAMILIARITY AND THE AGE OF THE NEST-SITE

S. ARON (1), J.M. PASTEELS (1), J.L. DENEUBOURG (2) and J.L. BOEVE (1)

*(1) Departement de Biologie Animale et Cellulaire, CP 160.*
*(2) Service de Chimie Physique II, CP 231, Université Libre de Bruxelles, 1050 Bruxelles, Belgium.*

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## *SUMMARY*

*Leptothorax unifasciatus* workers differentiate new areas from those previously explored. Indeed, a " coming and going " behaviour appears more frequent on a virgin paper than on a familiar one. The decrease of activity on a new paper after some hours indicates that this species rapidly gets to known such an area in the experimental device used here. The experiments suggest that the area is chemically modified by the ants' activity, but the possibility of a specific marking behaviour was not further investigated.

Three factors control the level of foraging activity in *L. unifasciatus* :

1°. The nature of the foraging area (familiar or virgin).

2°. The size of the society.

3°. The age of the nest-site.

Societies newly established in their nest show a higher level of foraging activity on a virgin area than on a familiar one. In every case, there is a linear relation between the size of the society and its activity. Long-settled societies always show a lower activity than recently established ones, and no difference was observed when they recruited on a virgin and a familiar area. Moreover, the society size appears to be less important in determining the general level of activity than for recently-settled societies.

These results are tentatively interpreted in eco-ethological terms, taking into account a main biological characteristic of *Leptothorax* societies : frequent nest emigrations that are either seasonal or due to fragile nest-sites.

## *RESUME*

**Recrutement alimentaire chez** Leptothorax unifasciatus : **l'influence de la connaissance de l'aire de récolte et de la durée d'occupation du nid**

Les ouvrières de *Leptothorax unifasciatus* différencient de nouvelles aires de celles précédemment explorées. En effet, un comportement de « va-et-vient » apparaît plus fréquent sur un papier vierge que sur un papier familier à la colonie. La chute d'activité sur un papier vierge après quelques heures indique que ce dernier devient rapidement familier à la colonie dans le dispositif expérimental utilisé. Les expériences suggèrent que le territoire est modifié chimiquement par l'activité des fourmis, mais la possibilité d'un marquage chimique n'a toutefois pas été explorée.

Trois facteurs contrôlent le niveau d'activité de fourragement chez *L. unifasciatus* :

1° la nature de l'aire de récolte (connue ou inconnue) ;

2° la taille de la société ;

3° le temps de séjour de la société dans un même nid.

Des sociétés établies récemment dans leur nid montrent un niveau d'activité de fourragement plus élevé sur une aire de récolte inconnue que sur une aire familière. Dans tous les cas, il existe une relation linéaire liant la taille de la société et son activité. Des sociétés établies depuis longtemps dans un même nid montrent toujours une activité inférieure aux sociétés récemment établies. Aucune différence n'est observée entre une aire de récolte inconnue et familière. De plus, la taille de la société apparaît être moins influente sur son activité générale que pour une société récemment établie dans son nid. Ces résultats sont interprétés en termes éco-éthologiques, tenant compte d'une caractéristique biologique essentielle des sociétés de *L. unifasciatus* : les déménagements fréquents, saisonniers ou liés à la précarité des nids.


## INTRODUCTION

*Leptothorax unifasciatus* is a common medio-European Myrmicinae. It is a monomorphic and monogynic ant with naturally small societies of 100 to 300 individuals (exceptionally large societies of 900 workers were obtained in the laboratory), living in precarious nest-sites under stones and in rocks interstices (PLATEAUX, 1978). Nest emigration seems to be frequent in *Leptothorax* species in natural conditions (MÖGLICH, 1978), colonies settling into new territories. Like other *Leptothorax*, this species recruits nestmates by tandem-running and trail pheromone to sugar food-sources, new nest-sites, and virgin areas (LANE, 1977).

During our studies of *L. unifasciatus'* food recruitment dynamics, we discovered that the society's activity is strongly influenced by two conditions modified by nest emigration: territorial familiarity and age of the nest-site. The influence of those parameters on the foraging activity will be described in this paper. We will first demonstrate that *L. unifasciatus* is able to discri-

minate between new and familiar areas. Although this discrimination can only be explained by postulating that the area is chemically modified by the ants' activity, the possibility of a specific territorial marking is not further analysed here. Recruitment activity in long-settled societies and in societies that have recently moved will then be compared on familiar and virgin foraging area. The results are tentatively interpreted by considering the species' behavioural ecology.

## MATERIAL AND METHODS

All the experiments were performed on queenright *L. unifasciatus* societies collected from schists in the vicinity of Treignes (Belgium) during September 81 and June 85. The societies were reared in laboratory plaster nests disposed on polyvinyl areas (20 × 30 × 4 cm). The inner boards of the areas were coated with talc to prevent escape.

Societies were fed ad libitum with brown sugar solution by means of bottles stoppered with cotton, and cockroaches. Water was continually available near the nest. The societies were kept throughout the year in constant environment at 20°C, with 12 hours day — 12 hours night. In these laboratory conditions, brood of all stages including eggs was abundant all the year-round. The experiments were performed from January to October, all nests having been collected at least three months prior to their first experiment.

Two different sets of experiments were realized. Set 1 served to study the behaviour of the ants on new areas. Experiments were performed on recently installed societies (see below), which were never starved. The method was previously used by JAFFÉ *et al.* (1979). Two sheets of paper (5 × 5 cm) were placed 15 cm from the nest-entrance and 5 cm from each other, at least 3 days before experimentation. The number of ants on these familiar papers was then compared to that observed on freshly placed papers. Further details will be given in the text.

To study the alimentary recruitment dynamics in *L. unifasciatus*, set 2 was performed. We starved each society for 10 days before conducting food-recruitment experiments which lasted 180 minutes. Experiments were always conducted at the same time of day, from 10 h to 13 h. In each experiment, the societies exploited one food-source (1 M sucrose) placed on a foraging area (20 × 30 × 4 cm) connected by a bridge to the nest area. Each society's recruitment behaviour was observed on 2 types of foraging area: familiar (frequented by the society for at least 15 days), or new (clean, virgin area). The location of the nests in the laboratory and the geometry of the experimental set-up were kept identical. No visual cues were modified. The number of ants in the foraging area and around the source were recorded at intervals of 3 min.

Some societies were encouraged to move to a new nest site on the foraging area in the following way: high humidification and continual artificial illumination of the old nest for one week followed by removal of the glass sheet covering the nest cavity. The foraging activity of societies of different sizes and nest-site ages were compared.

When we refer in this article to the concept of nest-site age, whether in laboratory or natural conditions, we refer to the length of time during which an ant society has been settled in its present nest-site.

Statistical tests used were taken from SIEGEL (1956) and ROHLF and SOKAL (1981).

## RESULTS

**Discrimination between familiar and virgin areas**

We have studied if the ants were able to discriminate between a familiar and a virgin sheet of paper. The number of ants on each paper was reported every minute for 15 minutes, after each one of the five following phases :

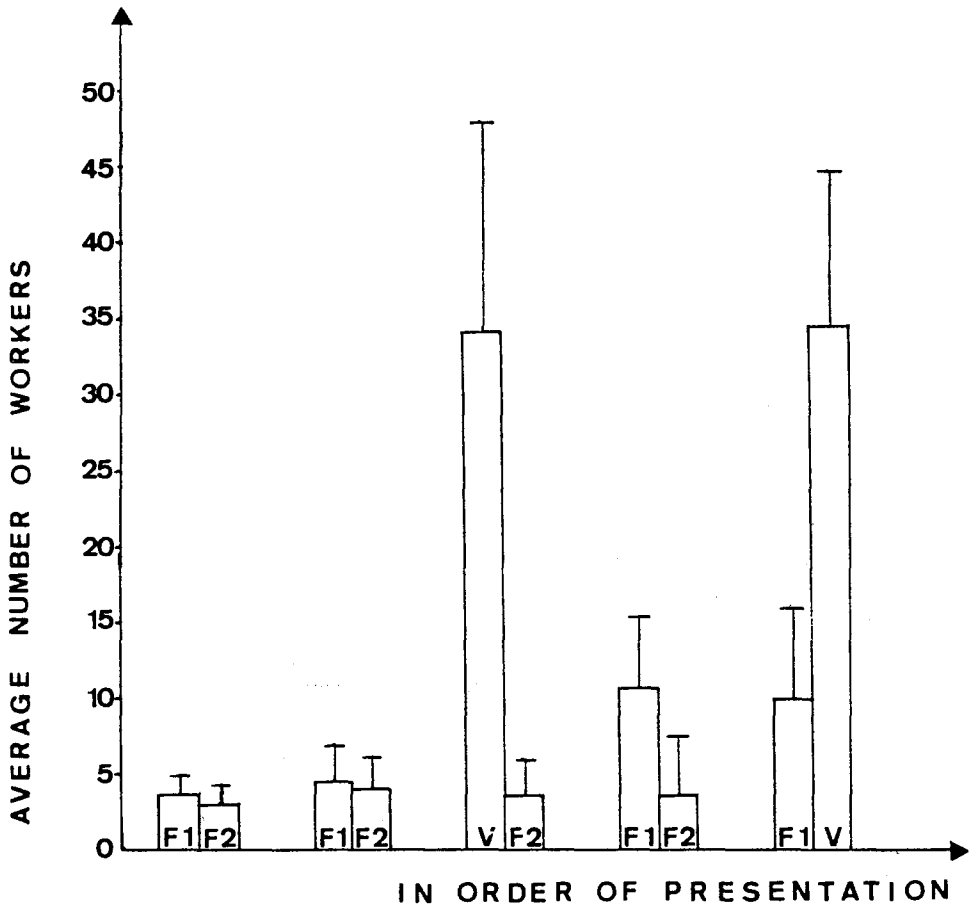


Fig. 1. — Average number of workers and standard error (N = 4) reported for two types of papers successively replaced over 15 min.
$F_1$ and $F_2$ : familiar papers.
V : virgin paper.

Fig. 1. — Nombre moyen d'ouvrières observé sur 15 min. et erreur standard (N = 4) pour deux types de papiers successivement remplacés.
$F_1$ et $F_1$ : papiers familiers.
V : papier vierge.

(1) the two familiar papers $F_1$ and $F_2$ are placed on the foraging ground ;

(2) $F_1$ and $F_2$ are removed and immediately replaced ;

(3) $F_2$ is put back, $F_1$ is replaced by a virgin paper (V) ;

(4) $F_1$ and $F_2$ are put back ;

(5) $F_1$ is put back, $F_2$ is replaced by a virgin paper (V).

*Fig. 1* presents the average number of ants on the above papers. We observed that the ants did not appear disturbed by our manipulations, and that the number of exploring ants increased on virgin paper. This high exploratory activity decreased when the new paper was replaced by a familiar one.

In 22 replicates, we compared the activity on two papers $F_1$ vs $F_2$ and $F_1$ or $F_2$ vs a virgin one. Two familiar papers already marked gave no significant difference between the number of ants walking on them ($P > 0.05$). On the other hand, ants were always more numerous on a virgin paper than on a familiar one ($P < 0.01$ ; Wilcoxon matched-pairs signed-ranks test). This high number of workers is not necessarily due to an exploratory recruitment. Indeed, we never observed tandem-running to new virgin papers. An explanation could be that ants stay longer on a virgin than on a familiar paper. The average values obtained were respectively 17.7 sec (S.D. = 17.2 sec, N = 50) and 11.7 sec (S.D. = 8.0 sec, N = 50) and were not statistically different ($P \sim 0.24$ ; Mann-Whitney U test). However, ants show a " coming and going " behaviour consisting of leaving the paper and immediately returning. This behaviour appears more frequently on a virgin paper than on a familiar one ($P < 0.00003$ ; Mann-Whitney U test). This behaviour induces us to measure the time spent by ants as follows : the total time spent by one ant on a paper = the total amount of time this ant was on the paper without leaving it for a distance greater than 1.5 cm. Only the time spent on the paper was taken into account. Whereas ants spend an average time of 15.1 sec (S.D. = 9.6 sec, N = 40) on a familiar paper, this value increases to 42.5 sec (S.D. = 29.8 sec, N = 40) on a virgin one. Such results are significantly different ($P < 0.00003$ ; Mann-Whitney U test).

In order to determine the lapse of time needed for a society to become familiar with the paper, one of the two familiar papers was replaced by a new one. We measured the activity on each paper every 5 min during several hours.

The results obtained clearly show that after about 2 h 30 the ant population on the test paper was already the same as on the control (*fig. 2*).

These results demonstrate that *L. unifasciatus* workers differentiate new areas from those previously explored, most probably by means of chemical cues. Indeed, all papers were identical in every respect before they were deposited on the nest area. Familiar paper must be chemically

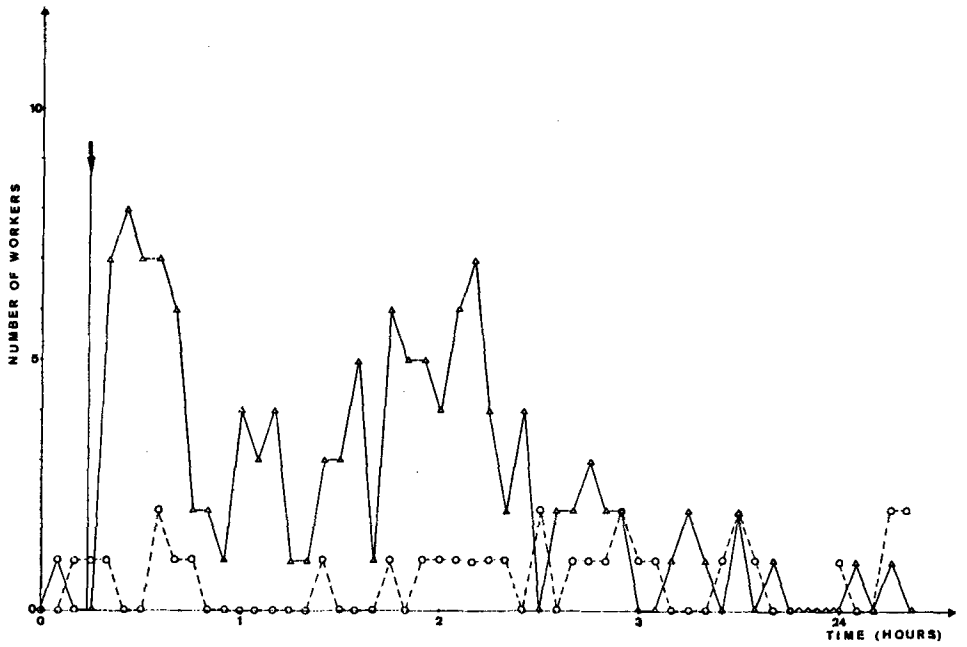


Fig. 2. — Time evolution of the number of workers on two papers. The arrow indicates replacement of one familiar paper by a virgin one.
O : familiar papers.
△ : virgin paper.

Fig. 2. — Evolution temporelle du nombre d'ouvrières sur 2 papiers.
La flèche indique le remplacement d'un papier familier par un papier vierge.
O : papiers familiers.
△ : papier vierge.

different from virgin paper, and this chemical modification can only result either directly or indirectly from the activity of the ants exploring the papers.

**Foraging recruitment**

When *L. unifasciatus* workers discovered a food-source, they recruited nestmates using tandem-running and trail pheromone (LANE, 1977 ; DE GEYTER, 1982).

In 32 experiments, the food-recruitment dynamics on a familiar and a virgin area were studied for 11 societies of different sizes and nest-site ages : societies installed in their nest for at most one month (recently-installed societies) and societies installed in their nest for more than one month (long-settled societies). Preliminary analysis showed that the choice of one month was appropriate to differentiate the two groups of societies.

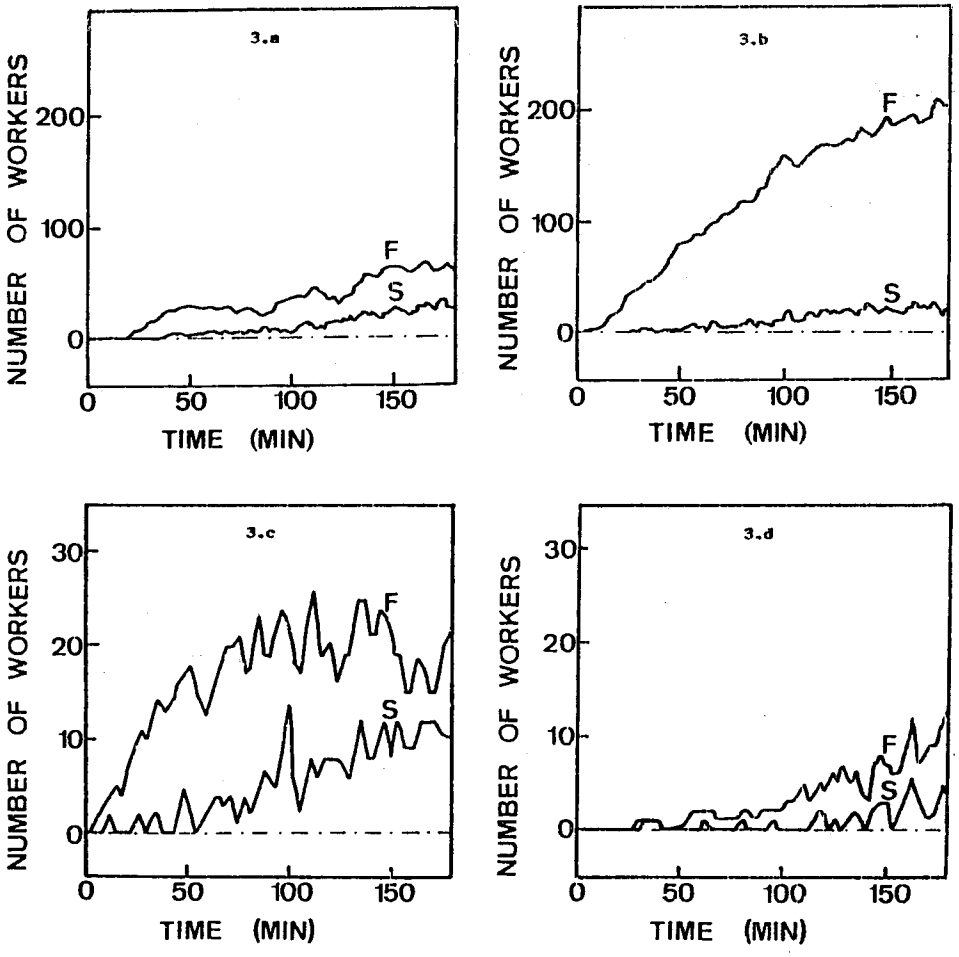


Fig. 3. — Time evolution (in min) of the number of workers on the foraging area (F) and around the food-source (S)
— for the recently-settled society B (950 workers) on a familiar area (3.a) and a virgin area (3.b) ;
— for the small recently-settled society D (300 workers) on a virgin area (3.c). Access to a virgin area elicited no activity in small long-settled societies.
— for the populous society B (900 workers) on a virgin area, 10 months after nest-moving (3.d).

Fig. 3. — Evolution temporelle (en min.) du nombre d'ouvrières sur l'aire de récolte (F) et à la source de nourriture (S)
— pour la société B (950 ouvrières) récemment installée dans son nid, sur une aire familière (3,a) et sur une aire vierge (3.b)
— pour la société D (300 ouvrières) récemment installée dans son nid, sur une aire vierge (3.c). L'accès à une aire vierge n'entraîna aucune activité pour des petites sociétés établies depuis longtemps dans un même nid.
— pour la société B (900 ouvrières) sur une aire vierge, 10 mois après son déménagement.

From the beginning of the experiments, the ant population in the foraging area and around the food-source grew more or less rapidly towards a plateau value (which is determined by the average population calculated for the last 60 min of experimentation). Some experiments discussed later on are illustrated in *figure 3*.

The foraging activities of the two groups of societies gave quite different results. For recently-installed societies, the number of workers observed on the foraging area at the plateau value increased considerably according to wether the area familiar or virgin. This difference became more pronounced according to the size of the society (see *fig. 4*). Indeed, regression lines 1 and 2 show the existence of a sgnificant linear relation binding the size of the society and its activity. Moreover, the variations in activity according to the society size appear statistically different if the area is virgin or familiar. A comparison of the confidence limits of the slopes of the two lines show that they are significantly different at the 95 % level.

For long-settled societies, the colony size seems not to be a determinant parameter controlling their activity, whatever the nature of the foraging area. The correlation coefficients are positive but not statistically significant. The low level of activity of long-settled societies should be stressed and of course quantitative trends are the more difficult to demonstrate. No significant difference of the total number of workers recruited to a familiar or a virgin area was observed. A comparison of the level of activity on the two types of foraging area between nests of similar sizes ($225 \leqslant N \leqslant 750$) shows no significant difference ($P > 0.05$ ; Mann-Whitney U test).

When the number of ants feeding are compared, a significant linear relationship with colony size is again observed for recently-settled societies, but not for long-settled societies (*fig. 5*). However no difference was observed for both type of societies according to the kind of the areas on which they foraged. This demonstrates that the the higher level of activity reported above for recently-settled societies foraging on virgin area results from the high number of recruits which explored the new foraging ground without collecting food.

A remarkable result is the decrease of the level of general activity for long-settled societies. This contrast stands out particularly when we followed the societies' recruitment dynamics on a virgin area. Food recruitment was studied on such an area for five societies of different nest-site ages. Two experiments are illustrated on *figure 3*. A small long-installed society which completely avoided a virgin area (it was observed that the ants reaching the virgin area turned back on the bridge rather than penetrate it) showed an increased activity in the same experimental situation, after it was induced to move into a new nest (see *fig. 3c*). Inversely, all the very active recently-installed societies showed some months after their nest-

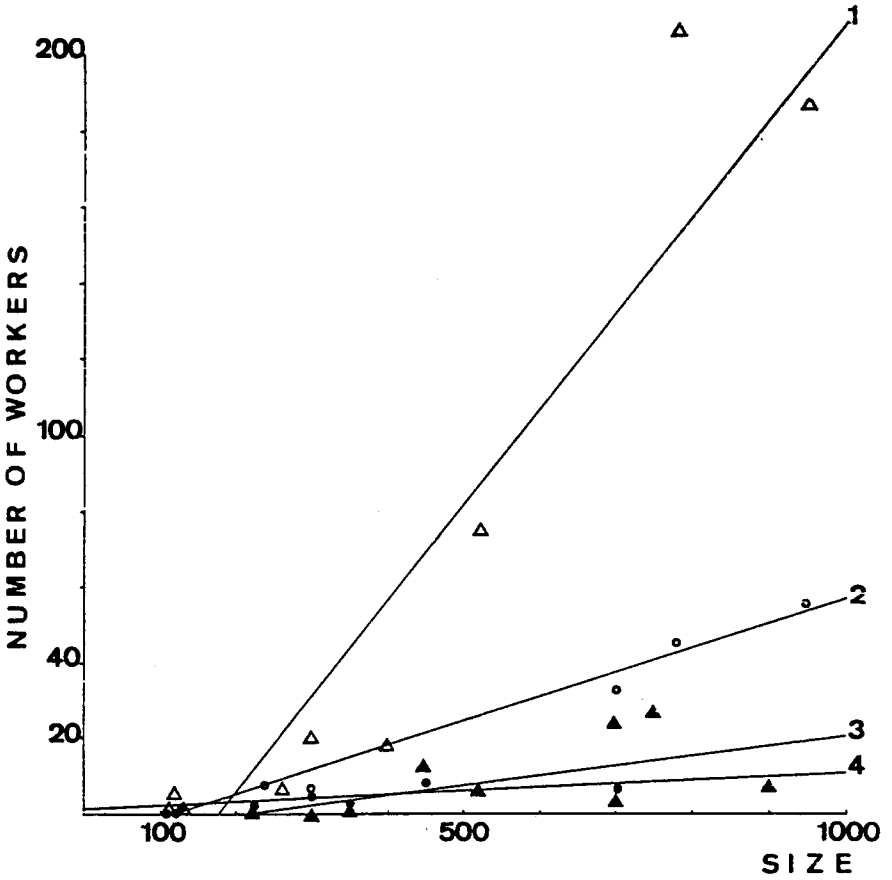


Fig. 4. — Comparison between the average number of workers observed for the last 60 min of experimentation on a familiar and a virgin foraging area for recently-settled and long-settled societies of various sizes.
Regression lines 1 and 2 of recently-settled societies recruiting respectively on a virgin (△) and a familiar (O) area are
$Y_1 = 0.25\ x_1 - 44$ ; $r_1 = 0.94$ ; $P < 0.001$
$Y_2 = 0.07\ x_2 - 8$ ; $r_2 = 0.99$ ; $P < 0.001$
The 95 % confidences limits of the two slopes are |0.33 — 0.18| for line 1 and |0.07 — 0.06| for line 2.
Regression lines 3 and 4 of long-settled societies recruiting respectively on a virgin (▲) and a familiar (●) area are
$Y_3 = 0.03\ x_3 - 6$ ; $r_3 = 0.61$ ; N.S.
$Y_4 = 0.01\ x_4 + 2$ ; $r_4 = 0.66$ ; N.S.

Fig. 4. — Comparaison du nombre moyen d'ouvrières observées au cours des 60 dernières minutes de l'expérience sur une aire de récolte familière et sur une aire vierge pour des sociétés récemment établies dans leur nid et pour des sociétés installées depuis longtemps.
L'abscisse est la taille de la société.
Les droites de régression 1 et 2 des sociétés récemment installées recrutant respectivement sur une aire vierge (△) et sur une aire familière (O) sont :
$Y_1 = 0.25\ x_1 - 44$ ; $r_1 = 0.94$ ; $P < 0.001$
$Y_2 = 0.07\ x_2 - 8$ ; $r_2 = 0.99$ ; $P < 0.001$
Les limites de confiance à 95 % des 2 pentes sont |0.33 — 0.18| pour la droite 1 et |0.07 — 0.06| pour la droite 2.
Les droites de régression 3 et 4 des sociétés établies depuis longtemps dans un même nid, recrutant respectivement sur une aire vierge (▲) et sur une aire familière (●) sont :
$Y_3 = 0.03\ x_3 - 6$ ; $r_3 = 0.61$ ; N.S.
$Y_4 = 0.01\ x_4 + 2$ ; $r_4 = 0.66$ ; N.S.

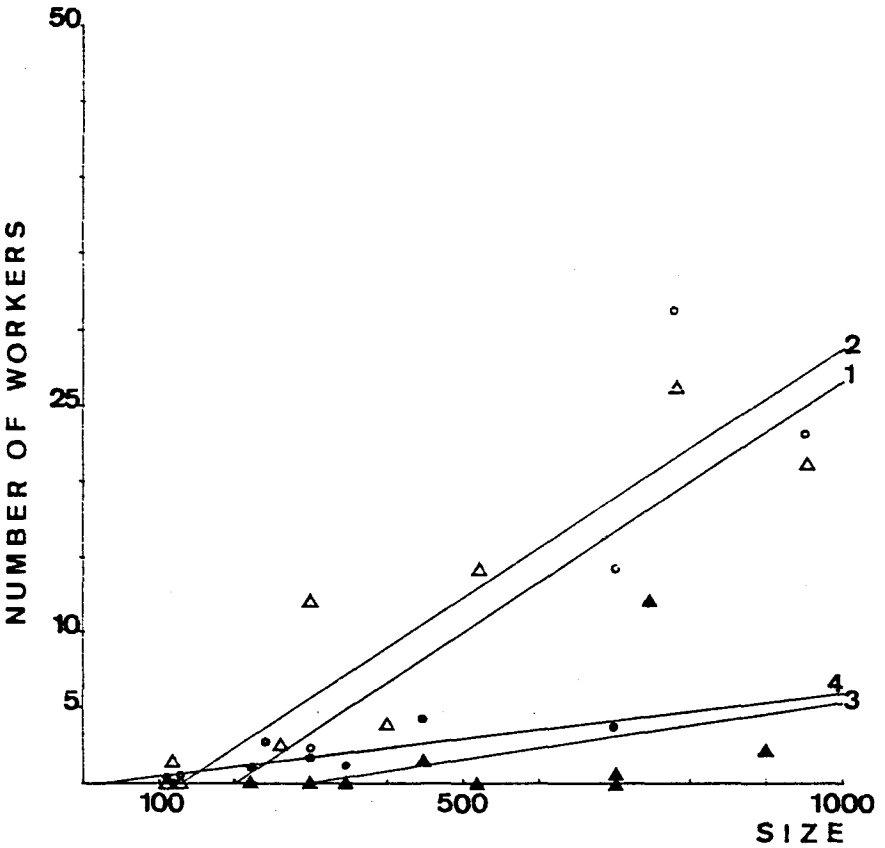


Fig. 5. — Comparison between the average number of workers at food-source observed for the last 60 min of experimentation on a familiar and a virgin foraging area for recently-settled and long-settled societies of various sizes.
Regression lines 1 and 2 of recently-settled societies recruiting on a virgin (△) and a familiar (O) area are
$Y_1 = 0.03\ x_1 - 3$ ; $r_1 = 0.91$ ; $P < 0.01$
$Y_2 = 0.03\ x_2 - 4$ ; $r_2 = 0.92$ ; $P < 0.01$
The 95 % confidence limits of the two slopes are |0.04 — 0.02| for line 1 and |0.05 — 0.02| for line 2.
Regression lines 3 and 4 of long-settled societies recruiting respectively on a virgin (▲) and a familiar (●) area are
$Y_3 = 0.007\ x_3 - 2$ ; $r_3 = 0.44$ ; N.S.
$Y_4 = 0.006\ x_4 - 0.3$ ; $r_4 = 0.76$ ; N.S.

Fig. 5. — Comparaison du nombre moyen d'ouvrières à la source observées au cours des 60 dernières minutes de l'expérience sur une aire de récolte familière ou vierge pour des sociétés récemment établies dans leur nid, et pour des sociétés installées depuis longtemps.
L'abscisse est la taille de la société.
Les droites de régression 1 et 2 des sociétés récemment installées recrutant respectivement sur une aire vierge (△) et sur une aire familière (O) sont :
$Y_1 = 0.03\ x_1 - 3$ ; $r_1 = 0.91$ ; $P < 0.01$
$Y_2 = 0.03\ x_2 - 4$ ; $r_2 = 0.92$ ; $P < 0.01$
Les limites de confiance à 95 % des 2 pentes sont |0.04 — 0.02| pour la droite 1 et |0.05 — 0.02| pour la droite 2.
Les droites de regression 3 et 4 des sociétés établies depuis longtemps dans un même nid, recrutant respectivement sur une aire vierge (▲) et sur une aire familière (●) sont :
$Y_3 = 0.007\ x_3 - 2$ ; $r_3 = 0.44$ ; N.S.
$Y_4 = 0.006\ x_4 - 0.3$ ; $r_4 = 0.76$ ; N.S.

moving a considerable decrease in activity on a virgin area (compare *figs. 3b and 3d*).

It has been reported (PLATEAUX, 1970) that *L. nylanderi* exhibits a fall of activity from November to January despite the constant laboratory environment. However, all the statistical tests performed to show a relationship between the societies' activity and the seasonality were inconclusive. No experiments were performed in November and December and the highest activity level was observed in January for recenly moved societies. If a small effect due to seasonality did occur it was certainly masked by other factors influencing the *L. unifasciatus'* foraging activity : the familiarity of the foraging area and the nest-site age.

## DISCUSSION

In *L. unifasciatus,* the foragers react quite differently to a familiar or a virgin area. In every case, a virgin paper induced a " coming and going " behaviour of the workers which entailed an increased activity on such a paper. A similar " territory choice " has been reported by ROISIN (1982) for the territorial species *Tetramorium impurum* : the workers " chose " to stay on a virgin paper rather than to leave it. Our results show that *L. unifasciatus* rapidly becomes familiar with a new area, taking only a few hours for a small surface close to the nest. The experiments were designed so as to eliminate any possible cues (textural or visual) but chemical ones. There is no doubt that the papers are chemically modified by the ants' activity which perceive and react to these modifications. This suggests that *L. unifasciatus* could be territorial and mark its territory. This possibility deserves more investigation. There is some evidence in the literature indicating that other *Leptothorax* species are territorial.

BUSCHINGER *et al.* (1980) reported that scouts of the slavemaker *Harpagoxenus sublaevis* perceive the previous presence of its host species, *Leptothorax acervorum,* in a given territory. For *Leptothorax ambiguus, L. curvispinosus,* and *L. longispinosus* (ALLOWAY, 1980) and for *L. muscorum* (STUART and ALLOWAY, 1982, 1983), territorial fights are reported.

Our results show that the foraging recruitment dynamics vary considerably according to the type of foraging area, the state of the society, and its size.

The length of time that ants have inhabited their nest greatly influences the general activity of the society. On the one hand, the level of general activity of the recently-installed societies was always greater than that of the long-installed societies. On the other hand, recently moved societies showed a higher level of activity on a virgin area than on a familiar one. Two complementary explanations could be presented to account for the high number of workers on the virgin foraging area :

1°) More ants are recruited on a virgin area, and a smaller proportion arrive at the food source. DE GEYTER (1982) showed that the recruitment accuracy (the ratio between the number of ants reaching the food source and the number of ants leaving the nest) varies considerably with the nature of the foraging area, independently of any possible visual cue (62 % in a familiar area — 18 % in a virgin area).

LANE (1977) observed the existence of an exploratory recruitment to new virgin areas leading to the dispersion of workers. De Geyter's results could therefore be partly due to the combination of an exploratory and an alimentary recruitment in a virgin area.

2°) The ants stay longer in a virgin than in a familiar area.. The shapes of the curves in *figures 3.a and 3.b* strongly suggest this possibility. Whereas the number of ants reached a plateau value after about 100 min for a familiar area, this number still increased after 180 min in the virgin area, suggesting that the area acts as a " trap " for the foragers which spend a long time exploring it before returning to the nest.

Long-settled societies show no significant difference in their reactions. Our experiments show that the length of time during which the ants have inhabited their nest has a greater influence on their activity than their absolute sizes. Two societies of different sizes, but which have been established in their nests for a long time, are more alike in their behaviour than two societies of the same size, but which have been established for different periods of time.

We know nothing of the mechanisms responsible for these behavioural differences in the worker's exploratory and foraging activities. The moving itself apparently raises the general level of activity of the society, which appears more " unstable " than a long-installed society. An alternative or complementary hypothesis is that a new nest has less drawing power on the workers than an old nest strongly impregnated with the society's odours. Indeed we have observed that it is very difficult to induce the emigration of a long-established society. The nest must literally be destroyed and opened to induce moving. The chemical marking of the nest may encourage the workers to remain inside, and the society may appear more " stable " Experiments are needed to test the influence of this possible marking on the foragers' behaviour.

*Leptothorax unifasciatus* nests in precarious sites without building complex nest structures. Nest emigrations could thus occur in nature after accidental destruction of the nests. These accidents could well be experienced by many species of *Leptothorax* (MÖGLICH, 1978). Seasonal emigrations were also reported in *L. unifasciatus* (DU MERLE *et al.*, 1978), and natural populations of *L. unifasciatus* seem to be characterized by a high though locally variable nest density, a situation very similar to that described by MÖGLICH (1978) for the North American *Leptothorax rugatulus*. Many of

the laboratory situations considered in this paper could thus reproduce natural situations. In nature, we must expect to encounter societies settled in their nests for various periods of times and societies which have recently emigrated into a virgin territory. We may suppose that the reactions of the ants in nature would be qualitatively similar to those reported in the laboratory. A hypothetical eco-ethological interpretation which would stimulate field observations could then be proposed.

A society that has recently moved into a virgin territory shows above all an intensive exploratory activity of the unknown territory. This exploration is strengthened by the low accuracy of foraging recruitment observed in this situation. This tendancy is similar to that proposed by PASTEELS *et al.* (1982) and DENEUBOURG *et al.* (1983), whereby an optimal accuracy in foraging recruitment would maximise the foraging benefit via the discovery of new sources by "lost" ants. On an unknown, virgin territory, it may be of prime importance to discover the resources as soon as possible and to evaluate the milieu's richness. If the territory is rewarding, the society settles there. The more rewarding the territory, the longer the society stays in the same location (if they are not obliged to move with the seasons or for reasons of nest fragility) and the exploration of a more and more familiar territory decreases.

Finally, it should be stressed that, if the behaviour of the societies could be qualitatively similar in the laboratory and in nature, the intensity of their reactions may be quite different. The intensity and permanence of chemical marks due to the activity of the ants could be strongly dependent on the nature of the substrat and the climatic conditions.

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