

SPATIAL ORGANISATION IN THE ARGENTINE ANT *Iridomyrmex humilis* Mayr.

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SUMMARY

The access of *I. humilis* workers to a new, chemically unmarked terrain elicits a collective exploratory behaviour involving the formation of a chemical trail. The ants moving to and from their nest reinforce the trail as they move along, returning ants laying longer and more frequent marks. A theoretical analysis of the streak lengths' distribution suggests that the workers' trail-laying behaviour is not just a simple-chain Markovian process, although this constitutes a good approximation.

The way in which an exploratory trail becomes an alimentary trail underlines the strong link between the two processes. The study of a relation exploration/territoriality shows that *I. humilis* workers recognise new territories from those previously explored most probably by means of chemical cues.

Key words: *Iridomyrmex humilis*, exploration, trail-laying behaviour, territoriality, spatial organisation.

RESUME

L'accès des ouvrières d'*I. humilis* à un nouveau territoire entraîne une exploration collective par piste chimique. Les fourmis se déplaçant vers le nid et vers le nouveau territoire renforcent la piste, cependant la longueur et la fréquence des dépôts restent plus importantes lors de la phase de retour au nid. Une approche théorique de type géométrique de la distribution des fréquences des longueurs des dépôts suggère que le comportement de marquage n'est pas un simple processus Markovien, bien que ce dernier constitue une bonne approximation du mécanisme réel.

L'intégration des pistes alimentaires au réseau exploratoire indique l'étroite relation entre ces deux processus.

L'étude d'une relation exploration/territorialité met en évidence un marquage territorial chez *I. humilis* reposant sur des repères chimiques.

Mots clés: *Iridomyrmex humilis*, exploration, comportement de marquage, territorialité, organisation spatiale.

INTRODUCTION

The access of *Iridomyrmex humilis* workers to a chemically unmarked terrain elicits a recruitment associated with a collective exploratory behaviour. At the beginning, the workers explore randomly the part closest to the nest. As this exploratory zone progresses into the area, a trail extends from it to the nest, indicating a chemical trail formation.

The exploratory pattern and its dynamics have been described previously, and a mathematical model shows how it may be generated by the individual workers' simple trail-laying and following behaviour (Deneubourg et al., 1988, 1989).

We present here three aspects of the *Iridomyrmex humilis* societies' spatial organisation: the trail formation in collective exploration, the relationship between the exploratory and foraging activities, and their territorial marking behaviour.

METHODS

Trail formation

Trail formation was studied by monitoring the behaviour of ants crossing a cardboard bridge (15 cm long, 0.5 cm large) placed between the nest and a 0.8x0.8 m sandy virgin area. A camera fitted with macrolenses was mounted on a mobile wagon moving in a horizontal plane parallel to the bridge, and positioned so as to observe the ants from side-on. This allowed us to note when the gaster touched the substrate, assuming that the ants lay chemical marks each time their abdomen meets its reflection on the bridge. A frame-by-frame analysis (one frame = 0.04 sec.) allowed us to measure the length of each pheromone streak by multiplying the average number of frames during which the ant marked continuously by 0.04 sec and by the ants' velocity. The same operation was made for non-trailing streaks.

Exploratory and foraging activities

We starved *I. humilis* societies 4 days before inducing successively exploratory and alimentary recruitments. The societies were given access to a 2 square meter sandy virgin area; once the exploratory pattern formed, we introduced a food source either 20 cm to the side of the exploratory trail, or 20 cm to the side of the exploratory front. The path of the workers leaving the food source after feeding was recorded by video.

Territorial marking

The method was previously used by Jaffé et al. (1979), and Aron et al. (1986). Two sheets of paper (5 x 5 cm) were placed 15 cm from the nest entrance and 5 cm apart, at least one week before the experiments. The number of ants

and the workers' behaviour on these familiar papers was compared to that observed on freshly placed ones. Further details will be given in the text.

RESULTS

Trail formation

The observation of the ants crossing the bridge showed a trail-laying behaviour by workers both moving from and returning to the nest.

Samples of individuals crossing the bridge indicate that, whatever their direction, about 40 % laid no trail whatsoever.

When measuring the length of each pheromone streak, it appears that ants crossing the bridge towards the nest lay more pheromone than those moving in the opposite direction: not only the workers lay significantly longer marks ($X_1=0.19 \pm 0.03$, $n=13$; $X_2=0.1 \pm 0.01$, $n=17$; $df=28$, $p<0.05$, Student's t test) but furthermore the average distance between two streaks is shorter ($X_1=0.31 \pm 0.09$, $n=13$; $X_2=0.57 \pm 0.07$, $n=17$; $df=28$, $p<0.05$, Student's t test).

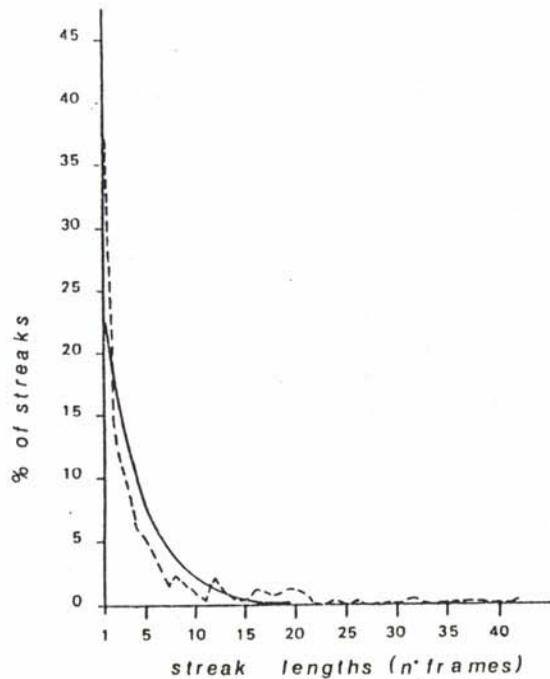
Pooling all streaks respectively both for ants moving to and from the arena, we estimated the probability q that a worker having marked k times lays one mark more, and $(1-q)$ that the ant stops marking. Both q and $(1-q)$ are assumed to be independent of k . This hypothesis means that the probability of an ant interrupting trailing remains constant with the length of streaks previously laid (n). So, the fraction of the number of streaks of length n is given by

$$F(n) = q^{(n-1)} (1-q)$$

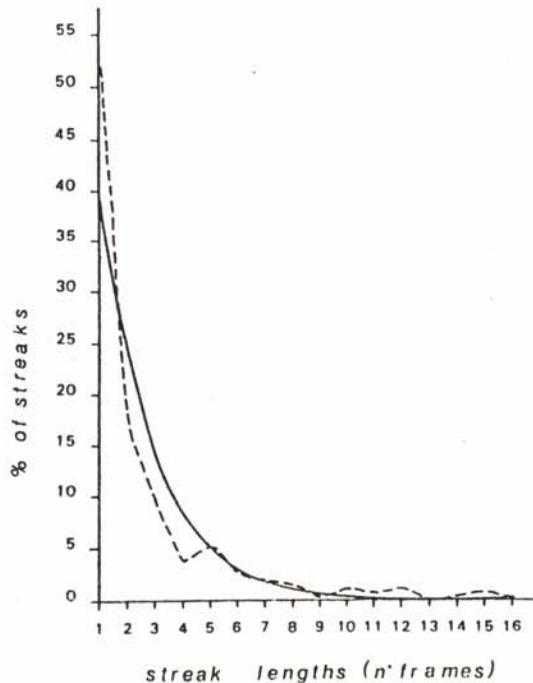
The comparison between the experimental and theoretical distributions of the streak lengths shows a strong analogy both for ants moving to and from the arena (figure 1). The discontinuity between the frequency of streaks of length 1 and those of a superior length is probably due to an over-estimation of their number (as it is not always clear if the ant is actually laying when only one frame in a row shows the gaster to be in contact with the bridge). This similarity suggests that the workers' trailing behaviour is probably not a single-chain Markovian process, although this constitutes a good approximation of the real process.

Exploratory and foraging activities

Observation established that workers crossing a bridge showed the same trail-laying behaviour both during foraging and exploratory recruitment. This strongly suggests that the same trail pheromone (Z-9-hexadecenal, a constituent of the secretion from the ventral Pavan's gland, Cavill et al., 1979, 1980) is used both during food and exploratory recruitment, and a continuity between the two processes.



(a)



(b)

Figure 1: Experimental (dashed curve) and theoretical (solid curve) streak length distributions for the ants moving towards the nest (a) and towards the area (b).

Figure 1: Distribution expérimentale (trait discontinu) et théorique (trait plein) de la fréquence des longueurs des dépôts pour les fourmis se déplaçant vers le nid (a) et se rendant sur le nouveau territoire (b).

This leads us to study the relationship between exploratory and foraging activities.

a) When placed near the exploratory trail, the food is rarely discovered. In most cases, the few foragers leaving the food source rejoin the exploratory trail when returning to the nest. They are however unable to divert other workers from the much stronger exploratory trail. As the food source is exploited, the alimentary trail is slightly reinforced, but never more frequented than the exploratory one.

b) When the food is placed 20 cm to the side of the exploratory front, its discovery is immediate. Rapidly, the ants are "captured" by the alimentary trail, and the workers' exploratory activity is displaced to the benefit of the alimentary activity. In this situation, exploration stops, and only some individuals are scattered on the area. In fact, both exploratory and alimentary activities were observed simultaneously with large societies (at least 2000 ants) when several exploratory trails appeared. In this case, the trails are independant and do not interact with each other.

Although little is known about this behaviour in natural conditions, we may reasonably suppose that the number of ants participating in an exploration is larger than tested in our laboratory experiments. In such a situation, the exploratory front could be sufficiently large to progress over the food source.

Territorial marking

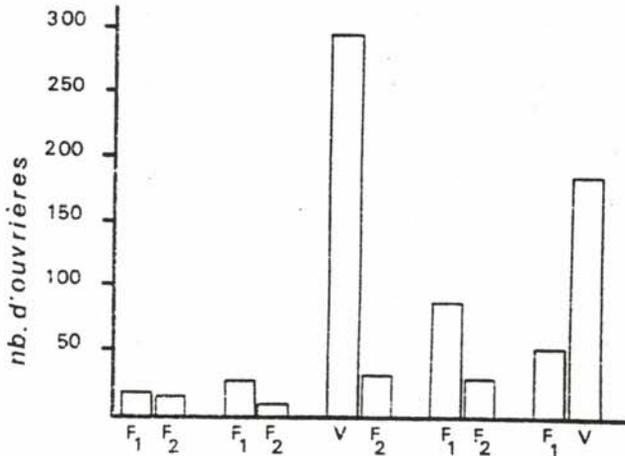


Figure 2: Number of workers reported for two types of papers successively replaced over 15 minutes. F₁, F₂: familiar papers. V: virgin paper.

Figure 2: Nombre d'ouvrières observé pendant 15 minutes sur deux types de papiers successivement remplacés. F₁, F₂: papiers familiers. V: papier vierge.

Figure 2 shows the number of ants reported each minute during 15 minutes for a familiar and a virgin paper. There is no difference in the number of ants on two familiar papers, and the ants did not appear disturbed by our manipulations. However, the number of exploratory ants increased significantly on a virgin paper. This high number of workers could be due to the fact that ants stay longer on a virgin paper than on a familiar one. The average values obtained (\pm standard error) are respectively 8.4 sec (\pm 1.3) and 4.8 sec (\pm 0.4), and are significantly different ($p = 0.015$, $n_1=n_2=40$; Mann-Whitney U test). Moreover, the ants show a "coming and going" behaviour more frequent on a virgin (3.7 ± 0.36 ; $n=20$) than on a familiar (1.0 ± 0.0 ; $n=20$) paper. This behaviour induces us to correct the time spent by the ants as follows: the total time spent 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. With this criteria, the ants stay longer on a virgin paper (31.6 ± 4.5 sec, $n=20$) than on a familiar one (6.0 ± 1.3 sec, $n=20$) ($p < 0.001$; 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. The results obtained (figure 3) clearly show that after about 4 hours the ant population on the test paper is already the same as on the control. As the activity on the virgin paper decreases, the time spent on the papers and the "coming and going" behaviour of the workers progressively falls. These results demonstrate that *Iridomyrmex humilis* workers distinguish new areas from those previously explored, most probably by means of chemical cues.

Some experiments on the territorial marking pheromones' life-time were then conducted by isolating a familiar paper from the society for various periods of time. Preliminary results indicate that no difference is observed between the number of ants on the experimental and control papers even if presented to the colony after one month of isolation. This indicates that the territorial marks are long lasting, and probably no longer corresponds to (Z)-9-hexadecenal.

During exploration, the trail-laying behaviour of the workers of the exploratory zone could constitute a territorial marking, and the ants reaction on a virgin paper would translate, at a smaller scale, what happens at this level.

DISCUSSION

The genesis of a collective exploratory behaviour in *Iridomyrmex humilis* corresponds to their highly agonistic and opportunistic behaviour. The chemical trails can lead to a rapid mobilisation of a large number of individuals to freshly discovered sources and/or to the colonisation of new sites, and constitute a massive and permanent defense

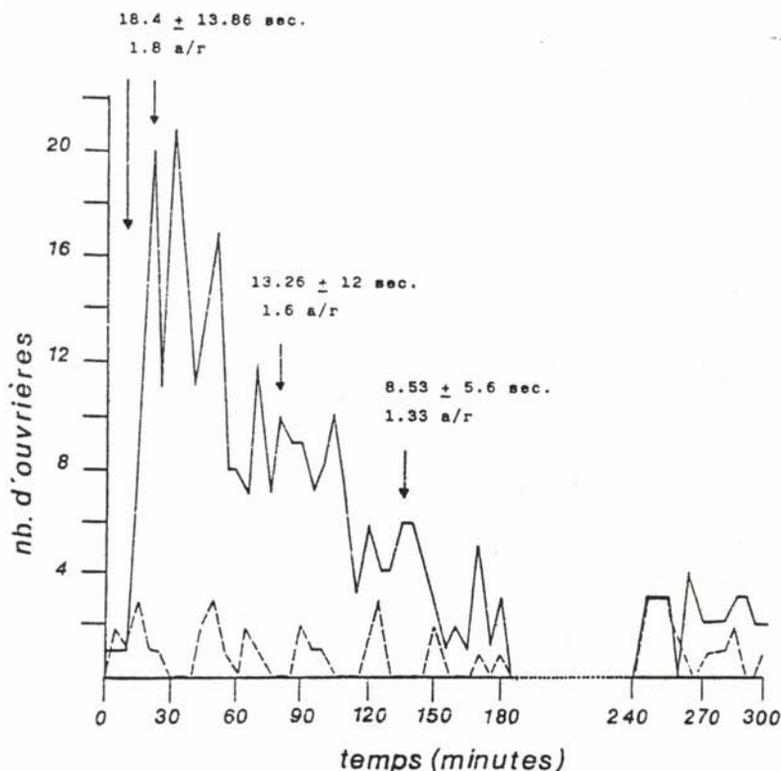


Figure 3: Time evolution of the number of workers on a familiar (dashed curve) and a virgin (solid curve) paper. Large arrow indicates replacement of one familiar paper by a virgin one. Small arrows indicate when the average time and standard errors spent by the ants on the virgin paper, and the "coming and going" frequencies are reported.

Figure 3: Evolution temporelle du nombre d'ouvrières sur un papier familier (trait discontinu) et un papier vierge (trait continu). La grande flèche indique le remplacement d'un papier familier par un papier vierge. Les petites flèches indiquent les moments auxquels le temps de séjour moyen et son écart type ainsi que la fréquence des aller/retours sont reportés.

against other competing ant species. Argentine ant colonies parcel into sub-colonies, establishing their nests near the sources, and staying interconnected by trails (Newell, 1909; Skaiffe, 1955; Markin, 1970). *Iridomyrmex humilis*' polydomous nests are not permanent structures, and movements of populations due

to unfavourable environmental conditions such as food-resource depletion, flooding or dessication (Markin, 1970; Wilson, 1971). Nest moving corresponds most frequently to seasonal migrations. The ants may then fuse with adjacent colonies, leading to the formation of one massive colony in a favorable location (Newell, 1909; Skaiffe, 1955; Benois, 1973).

The probable use of the same pheromone (Z-9-hexadecenal) both in food and exploratory recruitment suggests the involvement of only one pheromone in the Argentine ant societies' spatial organization: exploratory trails are initially important for the discovery of new food sources. Upon finding new sources, these trails then became food recruitment trails. As the colonies split up during divisional migrations, foraging trails are then used for nest moving near to the sources. With time, and with the evaporation/deactivation of the Z-9-hexadecenal, these trails no longer recruit but remains as guidelines or trunk trails used for traffic between the different sub-colonies. This extensive network would then constitute an extremely adaptative and stable territorial marking system.

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