

SPATIOTEMPORAL EVOLUTION OF THE TRAIL NETWORK IN *LASIUS FULIGINOSUS* (HYMENOPTERA, FORMICIDAE)

by

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SUMMARY

In *Lasius fuliginosus*, the existence of a permanent trail system, stable during a season and practically unchanged from one year to the next, was confirmed. These trails radiate from the nest and lead the foragers to trees and shrubs colonized by aphids where they collect honeydew. These aphid sites are also stable during a season and from one year to the next.

Other kinds of trails were observed : temporary honeydew collecting trails, temporary hunting trails and ephemeral recruitment trails. These trails, always connected to permanent trails, lead foragers respectively to temporarily exploited aphid sites, to large areas explored by ants and to large prey. Unlike permanent trails, they have a short life-time (several weeks for the temporary trails, some hours for the ephemeral trails) and they are not found in the same position from one year to the next. The temporarily exploited aphid sites are each year new ones originating, at least for a part of them, from the colonization of new sites by winged migrating aphids. They are thus spatially and temporally unpredictable food sources, like prey.

These results show that the ant *L. fuliginosus* combine a predictive foraging strategy (permanent trails) with an opportunist strategy (temporary and ephemeral trails).

Key words : *Lasius fuliginosus* — Ant-tended aphids — Permanent, temporary and ephemeral trails — Foraging strategy.

INTRODUCTION

Foragers of the ant *Lasius fuliginosus* (LATREILLES, 1798) travel along well defined, heavily frequented and long trails radiating from the nest, leading ants to aphid colonies where they collect honeydew which constitutes a major part of the *L. fuliginosus* diet (DOBZANSKA, 1966 ; GASPARD, 1967 ; HENNAUT-RICHE *et al.*, 1980). This trail network is remarkably stable : most of the trails persist during the whole season, remaining unchanged in the paths they take and moreover, they are re-established the next year after winter with great accuracy (HENNAUT-RICHE *et al.*, 1980).

L. fuliginosus is also characterized by a territorial specialization : using a mass marking technique, HENNAUT-RICHE *et al.*, (1980) have shown that foragers marked in summer on one of the two branches of a trail retained a high fidelity not only to the trail but also to the branch, for at least 12 days. They also had indications that trail fidelity persist throughout the winter.

The resource structure of the habitat is one of the major factors to which an ant foraging strategy is adapted (HÖLLDOBLER and LUMSDEN, 1980 ; ROSENGREN and SUNDSTRÖM, 1987). Persistency of the trails over long periods and high trail fidelity seem to be well adapted to the exploitation of stable food sources and is the expression of a predictive strategy (CHERIX and ROSENGREN, 1980).

In this paper, we present the results of a 3-years field study on the trail system of a *L. fuliginosus* colony. A detailed description of the trails and how they evolve, seasonally and from one year to the next, in relation to the kinds of food exploited is given so as to disclose patterns which give a better picture of the foraging strategy of these ants.

MATERIALS AND METHODS

Study area description

The *L. fuliginosus* nest was located in a cavity of a living tree, at the base of a cluster of hornbeams situated at the edge of a wood in the commune of Treignes (south-west of Belgium) and consisted of carton pulp (MASCHWITZ and HÖLLDOBLER, 1970). Although *L. fuliginosus* sometimes nest directly in the soil or under stones without making a carton nest, the majority of the nests are made of carton pulp and are located at the base of hollow trees (living or dead ones) (GASPAR, 1965). All the nests of *L. fuliginosus* we observed in the region were of that latter type. The wood was composed of various tree species : mainly hornbeams (*Carpinus betulus*) and oaks (*Quercus robur*) but also field maples (*Acer campestre*) and hazels (*Corylus avellana*). The south-east edge, where the nest was located, was bordered by a ground strip on which shrubs grew, mainly field maples (*Acer campestre*) and red dogwoods (*Cornus sanguinea*) (Fig. 1). Undergrowth was very scarce in the wood, and on the shrubby strip, rocky spaces were predominant.

Five aphid species provided honeydew for the ants : *Lachnus pallipes* (HARTIG, 1841) and *Stomaphis quercus* (LINNAEUS, 1758) on oaks, *Periphyllus obscurus* MAMONTOVA, 1955 on field maples, *Anoecia corni* (FABRICIUS, 1775) on red dogwoods and *Prociphilus bumeliae* (SCHRANK, 1801) on the single ash (*Fraxinus excelsior*) growing on the shrubby strip.

Field observations

The trail network of the nest was observed from March 1984 to September 1986. In 1984 and 1985, from late March to the end of November, a complete mapping of the trail network was carried out once a week. In 1986, the mappings were

undertaken at two or three weeks intervals. The trails were marked by means of small plastic sticks stuck in the ground every ± 20 cm.

During the seasons 1984, 1985 and 1986, each of the trees or shrubs growing in the territory patrolled by *L. fuliginosus* was searched visually for aphids and ants once a week. A shrub or a tree colonized by aphids and exploited by ants was easily detected either by the direct observation of ants milking the aphids or by observing columns of ants on the trunk of trees (the presence of numerous ants laden with honeydew in these columns was a sure indication of the presence of ant-tended aphid colonies on the trees).

In 1984, 1985 and 1986, the traffic on each of the permanent trails A, B, C, D (Fig. 1) was measured 4 times per week during the whole season (from April to November). The counting time was 5 min for each measurement of both outward and return flow. In the return flow, ants laden with honeydew (replete ants) or carrying prey were distinguished from empty ants (no honeydew, no prey). These measurements were performed between 4 and 5 p.m. Similarly, in 1985, weekly measurements were made of the ants' traffic on the temporary trails.

RESULTS

Every year, 4 types of trails were distinguished : permanent trails, temporary honeydew collecting trails, temporary hunting trails and ephemeral recruitment trails.

Permanent trails

Description and evolution during a season

Fig. 1 shows the permanent trail network as well as the trees and the shrubs colonized by aphids and exploited by *L. fuliginosus* during the three years of observation. Four main permanent trails could be observed every year (trails A, B, C, D — see Fig. 1). These trails led ants to trees and shrubs with aphid populations and they were intensely frequented by ants. From May to November, the traffic on each trail varied from ± 100 to ± 600 ants per 5 min (outward flow + return flows), depending on the trail and the time of the year and some 40 to 80 % of the ants in the return flow were laden with honeydew (replete ants). But, the function of the permanent trails was not only to lead ants to aphids and to bring back to the nest the produce of the harvest of the honeydew. They were also used as main routes by ants going to and coming from hunting in foraging areas both bordering permanent trails and located at their extremities (this point will be developed later). Two features of the permanent trail network distinguish it from the other types of trails : its spatial and temporal stability (permanence) during a season and its similarity from one year to the next.

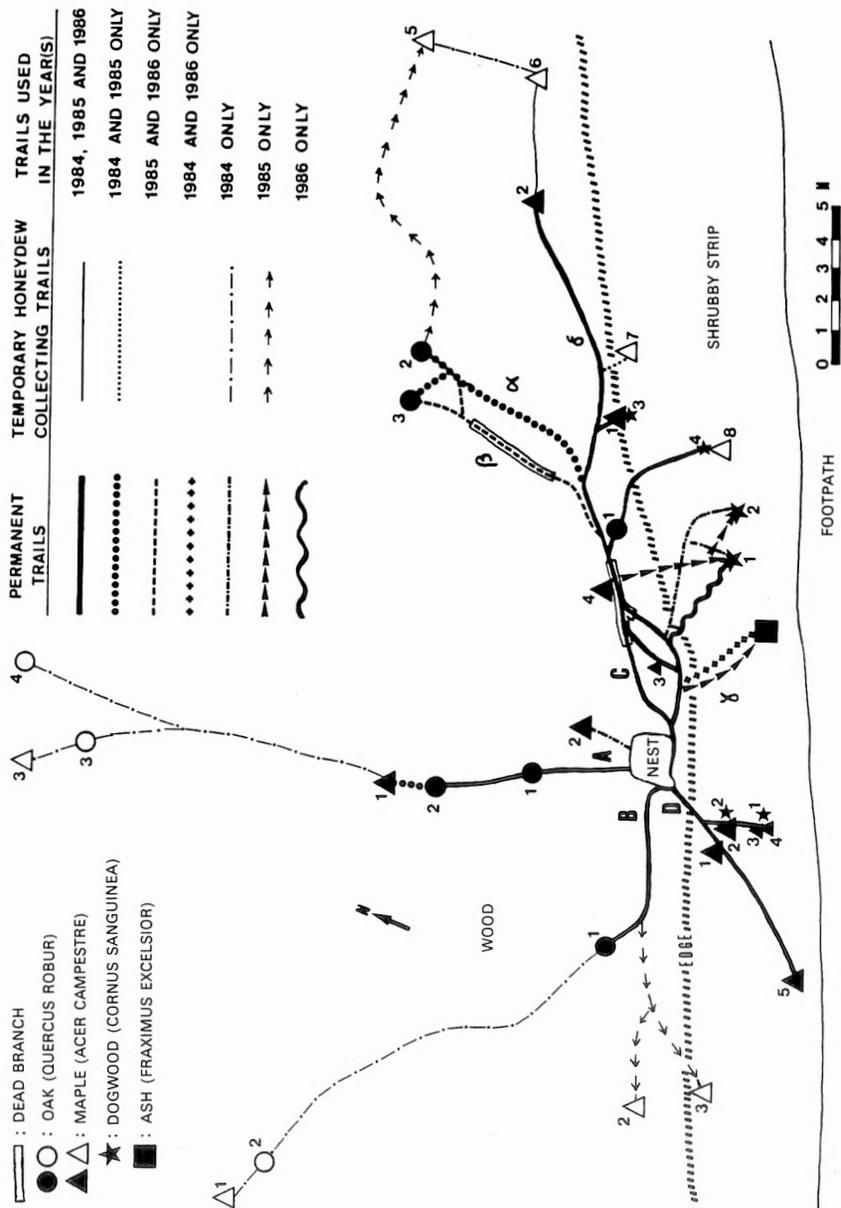
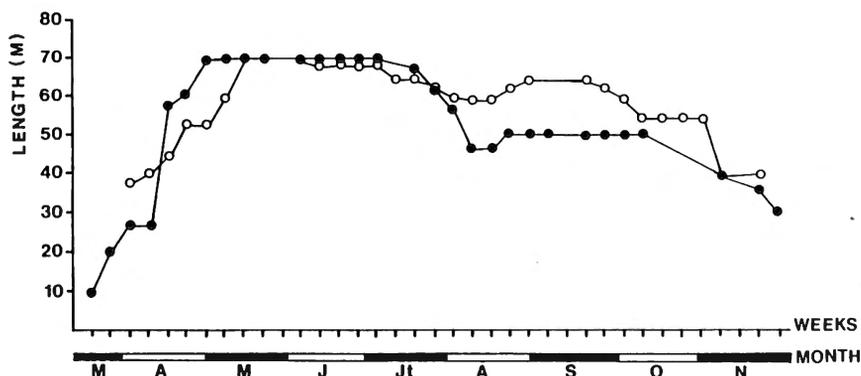


Fig. 1. — Permanent and temporary honeydew collecting trails network in 1984, 1985 and 1986. The capital and the greek letters next to trails designate respectively each of the main trails and sections of trails (see text). The solid symbols on the trails represent the permanent aphid sites and the open ones, the temporary aphid sites. The numbers next to the symbols refer to Table 1.

Permanence during a season

Each year, the first signs of the nest's activity were observed towards the end of March. The permanent network was progressively rebuilt during April reaching its full development at the beginning of May. It remained fully developed and unchanged in the paths taken by the trails and in length for most of the season of activity, shrinking somewhat in August (Fig. 2). The network progressively disappeared in November as the nest entered hibernation.



the flow of replete ants gradually decreased until the beginning of December when the ants became completely inactive.

Similarity from one year to the next

Fig. 1 shows the similarity of the permanent trail network during the three years: the foragers followed exactly the same paths every year. At the most we could observe some displacements to the right or left (generally no more than 10 cm) of small portions of the trails from one year to the next or during a season. There were, however, some minor variations in the paths taken by some lateral branchings of trail C. The main trunk of trail C, following the edge of the wood, was positioned in the same place every year. Its distal part, leading to the oaks labelled 2 and 3 in Fig. 1, deeper in the wood, changed with time. A new trail, β , replaced trail α in the course of the season 1985. This change can be explained by the existence in 1985 of a dead branch fallen on the ground during the winter 1984-85, making path β easier to follow than path α which was exclusively followed by the ants in 1984. Interestingly, this change was not immediate. In 1985, both α and β were followed by the ants and β supplanted α only at the end of August 1985. This suggests that in 1985 the memory of path α was strong enough to prevent some ants from following the easier path β . We speculate that in 1985 mainly naïve foragers followed path β . The next year, these workers would have retained their specialization to path β , progressively acquired the previous year. Some of the smaller lateral branchings leading to the shrubby strip also changed from one year to the next, without any obvious topographical interpretation.

Honeydew rewarding sites of the permanent trail network

Table 1 (see also Fig. 1) records all the trees and shrubs colonized by aphids and exploited by the ants on the permanent trails in 1984, 1985 and 1986; it also indicates the time during which they were exploited by ants. One can see the great stability of these sites during three years, with however some exceptions (see Table 1). Of the 24 honeydew collecting sites observed in 1984, 23 (96 %) were exploited again in 1985 and 20 (83 %) in 1986.

Of all the trees exploited by ants, the oaks were exploited for the longest time, all but one (oak 3 on trail C) being exploited during the whole season. They were colonized by *Lachnus pallipes* and *Stomaphis quercus*, two aphid species which completed their total life cycle, from spring to autumn, on the oak. They were ant-tended without interruption. The majority of the maples and the dogwoods were exploited by ants for periods exceeding three months every year (Table 1, Fig. 1). Maples were colonized by the aphid *Periphyllus obscurus* which lived from spring to autumn on its host and which was ant-tended during all its life cycle. We do not know the reason why some maples were deserted by aphids before autumn while, on others, the aphid populations managed to complete their entire life cycle. From April, the dogwoods were colonized by the aphid *Anoecia corni* whose colonies were invariably ant-tended. In July and August, the dogwoods were deserted by *A. corni*

otherwise not growing on the study area. In autumn, *P. bumeliae* was back on the ash where it laid sexuales. But unlike the sexuales of the aphid *A. corni*, they were not tended by the ants.

The result of the time-limited exploitation of some aphid sites located at the extremities of permanent trails, and due especially to the life cycle of some aphid species, is that some sections of the network disappeared before the end of the season. For example, section δ of trail C (Fig. 1) disappeared at the beginning of August 1984, the end of October 1985 and the end of June 1986. Section γ of trail C (Fig. 1) disappeared at the end of July 1984 and 1985, and at the end of June 1986 and finally, a small section of trail A disappeared in mid-July 1984 and 1985. The stability of the permanent trail network is thus related to that of the aphid sites.

Temporary honeydew collecting trails

Each year, at the beginning of the season (end of April and May), trails with a short life time (1-8 weeks) were formed by ants towards aphid sites always located outside the zone limited by the permanent aphid sites. These trails, always running on from the extremity of permanent trails (Fig. 1), had a low ant traffic and were poorly honeydew rewarding (the maximum replete ants flow was 15 ants/5 min). Each of these trails, except two of them, was recorded during only one of the three years. The temporary trail network was thus different from one year to the next (Fig. 1).

At least for some temporarily exploited aphid sites (maples n° 2, 3 on trail B and maples n° 5, 6, 7, 8 on trail C — little trees or shrubs whose foliage could be easily surveyed) we could observe how their exploitation by ants began, why they were poorly honeydew rewarding and how their exploitation ended. The beginning of the exploitation of these maples and the formation of the temporary trails leading to them was observed in mid-May and concurred with the arrival on these trees of numerous winged aphids (*Periphyllus obscurus*) which produced generations of apterous aphids. Furthermore, it was also in mid-May that numerous winged aphids (*P. obscurus*) were produced among aphid populations colonizing maples reached by permanent trails. Obviously, in this case, new maples were colonized by migrating winged aphids coming from permanent aphid sites and were then rapidly discovered by ants. Observation has shown that these apterous aphid populations, produced by migrating winged aphids, did not develop extensively on the newly colonized maples and rapidly declined, thus leading to the end of their exploitation by ants. The other temporarily exploited aphid sites (oaks n° 3, 4 and maples n° 3 on trail A, oak n° 2 and maple n° 1 on trail B) were big trees. Due to the difficulties in observing their foliage regularly, we were unable to know the history of the aphids colonizing these trees. But, as the exploitation of these aphid sites by ants also began in May, we can suppose, at least for the maples, that they were also colonized by winged migrating aphids.

From 1984 to 1986, a total of 11 aphid sites reached by temporary trails, and which we describe also as temporary (this is strictly true for at least 6 maples —

see above), were recorded. Only one was recorded each year and 3 during two successive seasons, the others having been recorded during only one of the three years (Table 1). It is interesting to note that maple 5 on trail C, exploited in 1984 and in 1985, was reached by a completely different temporary trail in each of the two years.

In summary, temporary honeydew collecting trails developed early in the season. As with the permanent trails, they led to exploited aphid sites, but, unlike permanent trails, were not similar from one year to the next, owing to the fact that the exploited aphid sites were not the same each year. The ant traffic and the amount of honeydew transported on these temporary trails was low. Some of these trails can be explained by the colonization of new sites by migrating winged aphids.

Temporary hunting trails

Each year, from April to mid-September, trails which never reached any aphid sites were observed. No replete ants were ever seen on these trails. On the other hand, ants carrying prey were frequent. These trails had a short life time (about 6 weeks) and they had a low ant traffic (about 30 ants/5 min, outward + return flows, with, on certain days, maximums of 60 ants/5 min). All along these trails, there was a constant leakage of foragers which explored the surrounding ground. Hunting trails were thus bordered by large areas which were constantly explored by varying numbers of ants according to the weather.

As can be seen from Fig. 3, hunting trails always developed from permanent trails, either from their extremities, which was the most frequent case, or from sections of permanent trails, closer to the nest. They ended either anywhere on the ground or, more frequently, at the foot of hornbeam clusters. A careful weekly examination of the ants' activity on the hornbeam clusters showed that they did not exploit aphids (or other food sources) on these trees. Instead, they scattered at their foot and they never climbed the trunks, except in April when the trail network was rebuilt and the exploratory behaviour was intense. Many hornbeams reached by the developing hunting trails were then climbed by ants and the same observation was made for hornbeams which were in the path of permanent trails. However, the ants climbing a hornbeam trunk were never numerous and they never formed columns like those observed on trunks of trees colonized by aphids. It was difficult to study the ants' activity above two meters in height; nevertheless, observations made on lower parts of these hornbeams gave an indication of what probably happened in higher parts. The ants were observed on many occasions licking hornbeam buds, and, on some occasions, sap exuding from bark. When the collection of sap ended in early May, the hornbeams were no longer climbed by ants but the trails reaching them did not disappear and became hunting trails. Thus, at least some hunting trails seem to have derived from the intense exploratory activity in April, when food is very scarce.

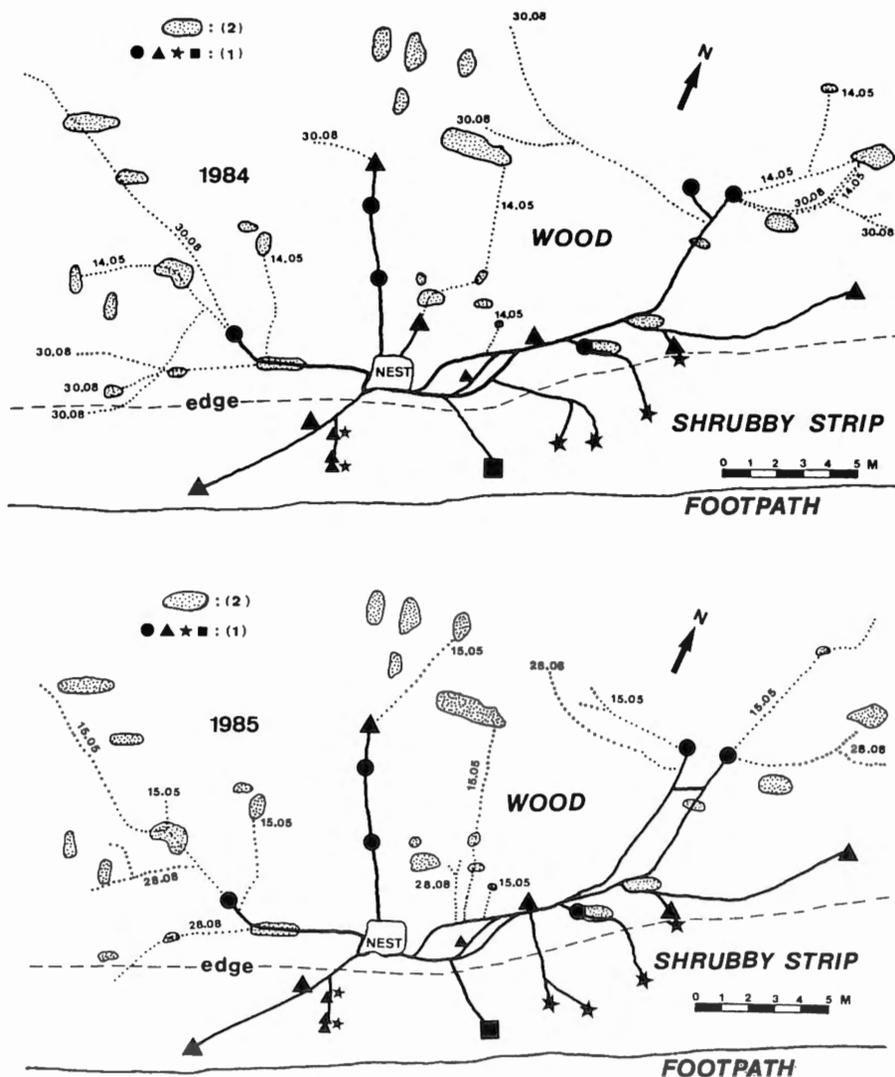


Fig. 3. — Main hunting trails observed between May and September in 1984 and in 1985. The dates on the hunting trails indicate when they were observed. : hunting trails ; ———— : permanent trails. Other symbols : (1) : aphid sites (see Fig. 1) ; (2) : clusters of hornbeams.

Fig. 3 presents the main hunting trails observed in 1984 and 1985, as they were at the height of their development. As can be seen, the hunting trail network was not the same from one year to the next. Moreover, it underwent modifications in the course of a season : trails disappeared after some weeks while others developed and all could vary in shape and length from week to week. The relative instability

of the hunting trail network both in the short and the long term, can be explained by the fact that, unlike the permanent trails which lead foragers to very localized and permanent honeydew sites, hunting trails lead ants to large areas of the territory which are individually explored in search of prey. Nevertheless, it can be seen from Fig. 3 that the general direction of hunting trails and the areas explored by these trails remained the same during a season and from one year to the next.

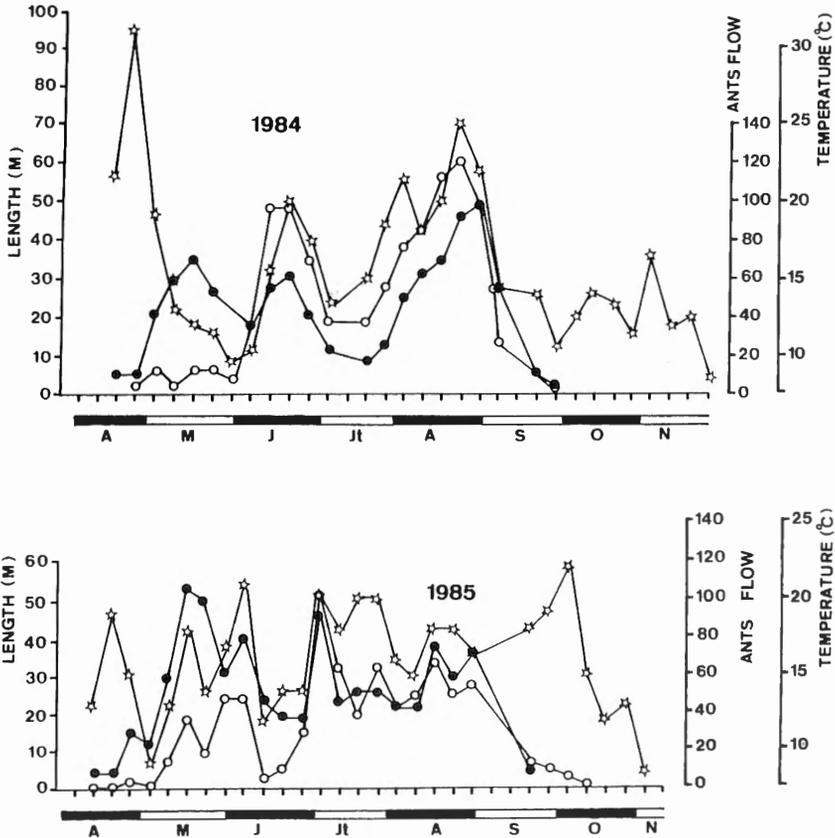


Fig. 4. — The change in the length of the hunting trails network over time (●) compared to the change over time of the weekly mean flow of ants carrying prey (per 5 min) on all the permanent trails (○) and the weekly mean soil temperature (☆).

Fig. 4 compares the changes in the values of three parameters with time : the hunting trail network length, the weekly mean flow of ants carrying prey on the permanent trails and the weekly mean soil temperature. Each year, the first hunting trails appeared in April. After a progressive lengthening, the hunting trail network attained a peak of development by mid-May. Afterwards, from mid-May to the end of August, it underwent periods of regression and extension. In September, it progressively regressed and by the end of September, had completely disappeared.

It was only during the period when hunting trails existed that ants carrying prey were observed on the permanent trails on which they constituted 5 to 15 % of the return flow. It can also be seen from Fig. 4 that there is a clear correlation between temperature and the two variables used to measure hunting activity.

Evolution of the whole trail network

Fig. 5 shows the changes with time in the length of the whole trail network (permanent + temporary, honeydew and hunting trails). It can be seen that it attained a maximum extension in mid-May. At that time, the permanent trail network was completely developed, the temporary honeydew collecting trails were fully developed and the hunting trail network attained a first maximum extension. A marked regression followed. It was largely due to the disappearance of the temporary honeydew collecting trails and to a regression of the hunting trail network, and to a lesser extent, to the disappearance of terminal sections of some permanent trails. Afterwards, the whole trail network underwent the same changes with time as the hunting trail network until the end of September when hunting trails disappeared. At the end of September, only the permanent trail network remained. In November the permanent trail network was progressively reduced from its extremities, and at the beginning of December the nest entered hibernation.

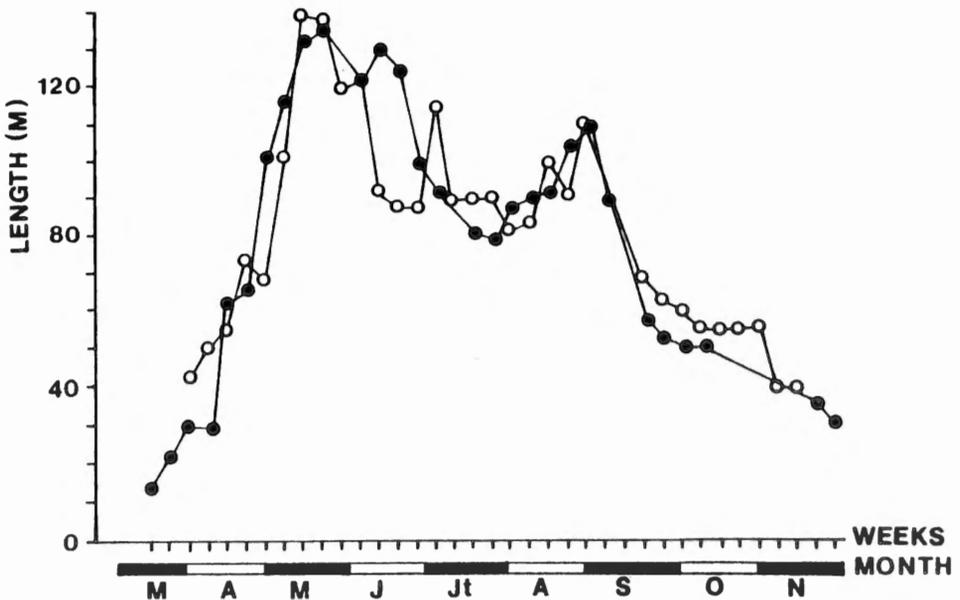


Fig. 5. — The changes in the length of the whole trail network with time in 1984 (●) and in 1985 (○).

Ephemeral recruitment trails

These trails were formed when the ants discovered a prey too large to be carried as such into the nest. Recruited ants cut up the prey and removed it piece by piece. Most of the prey collected in this way were earthworms, intensely hunted by *L. fuliginosus*. From the 90 observed prey which could not be carried by a single ant, 73 (81 %) were earthworms, 7 (7,7 %) large caterpillars and the remainder (11 %) consisted of occasional prey (adult moths, slugs, flies, maggots and centipedes). It was mainly from June to August that the ants heavily preyed upon earthworms (Table 2). In October and November, no ephemeral recruitment trails were observed.

Fig. 6 shows all the recruitment trails observed in 1984 and 1985. 51 % of them (N = 74) joined the permanent network at the level of a tree or shrub which could be used as an orientation cue. They lasted only the time needed to collect the prey (no more than a few hours) and never evolved into temporary hunting trails.

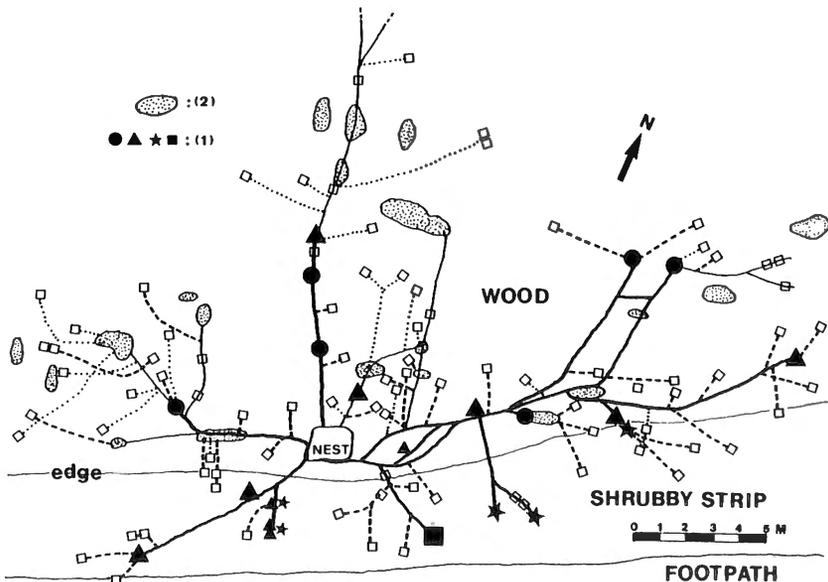


Fig. 6. — Ephemeral recruitment trails observed in 1984 (.....) and in 1985 (- - - -). — : long-lasting trails (permanent trails, temporary trails). □ : prey. Other symbols : (1) : aphid sites (see Fig. 1); (2) : clusters of hornbeams.

TABLE 2.

Number of earthworms captured by ants each month in 1984 and in 1985
(one month = 4 observations of the trails network of the colony).

Year	Month								
	M	A	M	J	Jt	A	S	O	N
1984	0	1	0	10	6	5	3	0	0
1985	0	3	2	8	26	8	1	0	0
TOTAL	0	4	2	18	32	13	4	0	0

Every year, we observed one or two raids conducted by *L. fuliginosus* on *Formica fusca* LINNÉ, 1758 colonies. On these occasions, similar recruitment trails were formed. They were heavily frequented, always linked to a permanent trail and led ants to the raiding place. The booty (brood and some sexuals) was brought to the nest along the recruitment trail and the permanent trail. These raiding trails, also observed by DOBRZANSKA (1966) in *L. fuliginosus*, only lasted one day.

DISCUSSION AND CONCLUSION

Confirming other observations (DOBRZANSKA, 1966 ; GASPAS, 1967 ; HENNAUT-RICHE *et al.*, 1980), we observed the existence of a heavily frequented permanent trail system, remaining unchanged over at least three years and leading ants to aphid sites. Furthermore, our observations revealed the existence of other kinds of trails in *L. fuliginosus* : temporary honeydew collecting trails, temporary hunting trails and ephemeral recruitment trails.

The permanent trail system of *L. fuliginosus* is related to very stable food sources ; here aphid colonies providing honeydew. Collection of honeydew through a trail system remaining unchanged for several years (topographic constancy) is found in other ant species like *Dolichoderus taschenbergi* (MAYR, 1866), *Formica obscuripes* FOREL, 1886 (BRADLEY and HINKS, 1968), *Camponotus modoc* WHEELER, 1910 (DAVID and WOOD, 1980) and wood ants of the *Formica rufa* LINNÉ, 1758 group (CHAVIN, 1962 ; ROSENGREN, 1971 ; MABELIS, 1979). In wood ants, ROSENGREN (1977) has shown that the topographic constancy was most likely determined by the existence of a true topographic tradition. During the season, the wood ant foragers show a high trail fidelity which persists through the winter and which is mainly caused by a long-term individual memory of spatially organized cues (trees, canopy, etc...) (ROSENGREN, 1971 ; ROSENGREN and FORTIELIUS, 1986). In spring, the trail system is rebuilt by the old specialized foragers. They recruit and guide on their trails the young, naïve workers which will become themselves specialized for particular trails later in the season (ROSENGREN, 1977). *L. fuliginosus* also shows a high trail fidelity during the season (HENNAUT-RICHE *et al.*, 1980). Short and long-term fidelity to trail will be the subject of a subsequent paper. There is an

obvious convergence in the foraging strategies used by wood ants of the *F. rufa* group and *L. fuliginosus*. That foraging strategy seems to be an adaptation to the exploitation of localized and stable food sources in space and time, such as aphid colonies. This is a predictive strategy which is also indicated by the fact that the permanent trail system was rebuilt in April when honeydew was not yet available (not until May). This latter observation was also made by ROSENGREN and SUNDSTRÖM (1987) and SUDD (1983) in wood ants (*F. rufa* group).

L. fuliginosus has also developed a foraging strategy adapted to the exploitation of unpredictable food sources in space and time. This opportunist strategy is particularly well exemplified by the ephemeral trails exploiting large prey (mainly earthworms in our study) and by the raiding trails. These trails are obviously recruitment trails similar to those experimentally observed by HANGARTNER and BERNSTEIN (1964) and HANGARTNER (1967).

The temporary honeydew collecting trails and the temporary hunting trails are other manifestations of an opportunist foraging strategy in *L. fuliginosus*. These trails exploit respectively aphid colonies established from winged migrating aphids and scattered small prey, two food sources therefore unpredictable in their location.

The reasons why the aphid sites reached by the temporary honeydew collecting trails were exploited during only some weeks and were poorly honeydew rewarding are still unknown. We nevertheless advance an hypothesis based on two observations : firstly, these aphid sites were always located at the extremities of the territory patrolled by the foragers (Fig. 1) and secondly, their appearance and their discovery by ants happened at a period of the season (end of April and May) when the ant flows on the permanent trails underwent a considerable increase following the appearance of the second aphid generation on the permanent aphid sites. It could be, therefore, that the collection of large quantities of honeydew on the permanent aphid sites mobilizes the major part of the forager force. Few ants would then be available for the exploitation of newly appeared food sources, less rich and located far from the nest. These aphid colonies either would be abandoned by the ants or would rapidly decline through lack of ant-attendance. It is well known that aphids derive benefits from ant-attendance : protection against natural enemies, increased reproduction rates, sanitary effects (removal by the ants of the excreted honeydew which otherwise could contaminate them) and some aphid species are unable to survive if they are not tended by ants (WAY, 1963).

Hunting trails have some similarities with the trunk-trails observed in harvester ants of the genus *Pogonomyrmex* and *Pheidole militica* WHEELER, 1915. The foragers of these ants travel on well established trunk-trails before diverging in individual excursions in search of seeds (HÖLLDOBLER, 1976 ; HÖLLDOBLER and MÖGLICH, 1980). In these harvester ants, a trunk-trail originates from a recruitment process following the discovery of a new rich foraging area. Its persistence varies from some days to several weeks, depending on the amount of seeds available. The trunk-trail is abandoned when the area is depleted of its seed supplies and a new one is established, leading to a new area. Hunting trails of *L. fuliginosus* also lead foragers to areas they individually explore in search of disseminated prey, as is the case with seeds, and are abandoned after some time while others are established.

Therefore, like trunk-trails in harvester ants, hunting trails could originate from recruitment trails and lead to areas where prey are abundant. This would suppose of course that the distribution of the prey is not homogeneous over the foraging area. However we have no information about this.

Another interpretation of hunting trails, not excluding the above hypothesis, is based on the observation that almost all the hunting trails originate from the extremity of permanent trails. Hunting trails would then represent a way of enlarging the hunting territory and of leading foragers to areas located outside those patrolled by permanent trails. This enlargement of the hunting territory could be a consequence of a depletion of prey in the vicinity of the nest or of an increased need in protein. While *L. fuliginosus* is active from early April to late November, the hunting trails and ants carrying prey on the permanent trails were observed only from the end of April to the end of September, with the most intensive periods being in June, July and August. It is interesting to note that it is only during the same limited period that earthworms are captured by ants (see Table 2).

The development of the hunting trail system seems to be, at least partly, regulated by the soil surface temperature, being all the more extensive when temperature is high (see Fig. 4). Soil temperature is known to affect forager activity in *Formica rufa*, either increasing their number (SKINNER, 1980) or their running speed (HOLT, 1955). Temperature could also influence the prey activity, thus increasing the frequency of meetings between foragers and prey. Nevertheless, temperature can not account for all variations in hunting activity. Indeed, in late April and May, the hunting trail network extended while temperature was still low (and even decreased in 1984) and few prey were carried back to the nest. During April and early May, food sources (honeydew and prey) are non-existent or very scarce and the foragers showed an intense exploratory behaviour. The collection of sap in April, as also observed in wood ants (*Formica rufa* group) (HORSTMANN, 1974; MABELIS, 1979; SUDD and SUDD, 1985; ROSENGREN and SUNDSTRÖM, 1987), is the expression of this search of the least food sources, which probably explains the extension of the hunting trail network in April and early May. Also, in October the hunting trails completely disappeared and no more ants carrying prey were observed although the temperature remained relatively high during the daytime, especially in 1985. Other factors must therefore account for the development of the predatory activity of *L. fuliginosus* in the course of a season. Such factors could be prey availability and the colony's need for protein. We know unfortunately nothing about the phenology of *L. fuliginosus* except that the swarming period occurs in June and July (GASPAR, 1967) (our observations have shown that the swarming period was in fact much longer and that it extended from mid-June to September each year).

It should be pointed out that hunting trails are not the only way whereby the foragers reach areas which they individually explore in search of prey. Indeed, observations have shown that during the hunting period (and mainly in July and August), foragers also explore the surrounding grounds all along the permanent trails. Therefore, it seems that the ants leave the trail system at any point (permanent trails or hunting trails) to explore the surrounding area. This observation is

very similar to that of HOLT (1955) who has shown that *Formica rufa* foragers can leave the trail system at any point along it, at random.

The ephemeral and the temporary trails are all linked up to permanent trails, and almost always to their extremity(ies) in the case of the temporary trails. The permanent trail system seems therefore to be the central axis of the mixed (predictive and opportunist) foraging strategy observed in *L. fuliginosus* : it leads specialized foragers to localized and predictable food sources and it is used as a base for the exploration of the surrounding areas. In this latter case, recruitment processes follow the discovery of food sources (new aphid colonies or prey) and trails are formed which, depending on the kind of food discovered, will be ephemeral or temporary.

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