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Research article

Spatial specialization of the foragers and foraging strategy in *Lasius fuliginosus* (Latreille) (Hymenoptera, Formicidae)

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Summary

The spatial specialization in *Lasius fuliginosus* was investigated in the field by a mass-marking of foragers with colors. In the spring, summer and autumn, foragers exhibit a high degree of persistence, with coefficients of fidelity between 83 and 96%, in using a particular foraging trail, in visiting a particular tree or shrub housing aphid colonies, and even micro-sites like a particular branch. A high degree of fidelity to particular temporary hunting ground areas has also been shown. Trail and aphid site fidelity persist for at least 1 to 3 months and are preserved through the hibernation period (about 5 months). However, in early spring, a period during which food sources are scarce, trail fidelity is lower (coefficient of fidelity: 57%).

Spatial specialization develops quickly in foragers recruited to a new permanent food source. Once acquired, the specialization is not rigid since specialized honeydew collectors can shift from a no more rewarding aphid site to other aphid sites of the same trail on which they develop a secondary specialization.

The ecological and behavioral aspects of the spatial specialization in *L. fuliginosus* are discussed with reference to the resource structure of the habitat.

Introduction

The foraging behaviors of ants have been classified into broad categories such as diffuse or individual foraging, recruitment, trunk-trails and group hunting (Oster and Wilson, 1978; Hölldobler and Wilson, 1990). As pointed out by Traniello (1989), this classification is to some extent artificial and "any one category must not be mistaken for a species-typical characteristic when in fact it may be a flexible component of the total foraging strategy". However, using the above-mentioned classification, the European ant *Lasius fuliginosus* falls in the trunk-trails category since its most remarkable foraging trait is the use of trunk trails radiating from the nest, channeling the foragers towards stable aphid colonies and hunting ground areas, and remaining unchanged for several years (Dobrzanska, 1966; Hennaut-Riche et al., 1980; Quinet and Pasteels, 1991).

A striking analogy exists between the foraging patterns of *L. fuliginosus* and those of the wood ants of the *Formica rufa* group. Both have populous colonies, build networks of stable foraging trails and their diet includes prey and honeydew collected throughout the year. They live in similar habitats – woody lands – and are territorial. Frontier's conflicts are observed when nests of both species occur in the same area (de Bruyn, 1978; Mabelis, 1984).

The foraging behavior of the wood ants is well documented. It was shown that the foragers exhibit a high degree of trail fidelity which does not decrease with time and which is preserved over the winter period (Rosengren, 1971; Mabelis, 1979; Cherix and Rosengren, 1980). The spatial fidelity extends to branch routes and to particular aphid trees as well as to hunting trails and possibly to hunting ground areas along the foraging trails (Dobrzanska, 1958; Rosengren, 1971, 1977b; Cosens and Toussaint, 1985). The existence of a "topographic tradition", i.e. the transfer of the topographical information about the routes from one generation (the old specialized foragers) to another (young naïve foragers) through recruitment, was demonstrated, and is generally seen as an adaptation to food sources with stable location like aphid colonies (Rosengren, 1971, 1977a; Cherix and Rosengren, 1980).

Although the foraging behavior of *L. fuliginosus* has been far less studied, it was shown that the basis of the foraging organization in *L. fuliginosus* is a similar partitioning of the foraging ground between specialized foragers (Dobrzanska, 1966; Hennaut-Riche et al., 1980): a strong trail fidelity persisting for at least two to three weeks was observed in summer, spatial specialization was observed at the level of a branch route and it was suggested but not definitely proved that the trail fidelity is preserved, at least partially, through the winter.

The aim of the present work was to further explore the level of spatial specialization of the foragers of *L. fuliginosus* when collecting honeydew: specialization on a foraging trail or an aphid-site, tree or shrub. Special attention will be given to the level of specialization in early spring after hibernation and to its development through time. Also, the spatial specialization of prey hunters will be investigated. Although the distribution of the honeydew sources is rather stable in space and time, some variations were observed. During the season, some sites are abandoned by the aphids, a consequence of the life cycle of those aphids, which requires them to develop on two successive host plants (Quinet and Pasteels, 1991). We will explore whether or not the foraging behavior remains flexible enough to cope with such seasonal development of food sources despite previous specialization.

Material and methods

The colony used for the experiments was situated at the edge of a deciduous wood in Treignes, in south-western of Belgium. The nest itself was located in a cavity at the base of a living hornbeam (*Carpinus betulus*), the dominant tree species in the wood. The other tree species were oaks (*Quercus robur*), field maples (*Acer campestre*) and hazels (*Corylus avellana*) while the undergrowth was very scarce. Shrubs, mainly field maples, red dogwoods (*Cornus sanguinea*), and an ash

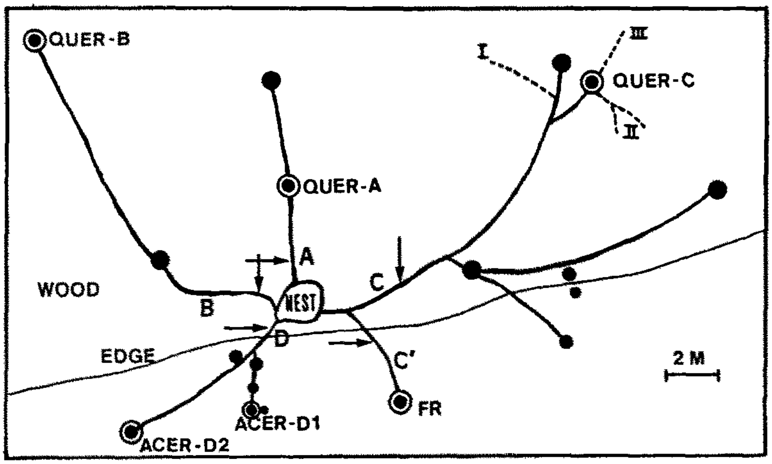

Figure 1. Schematic map of the permanent trails network observed from 1984 to 1986. Solid lines: main foraging trails. Dotted line: hunting trails on which ants were marked (see text). Little arrows: places of traffic counts on the main trails. Solid symbols: trees and shrubs where honeydew (or sugared water – see text) was collected by ants. The name placed next to a symbol and the circle around it indicate that ants were marked on the tree or shrub. Quer: oak; Acer: field maple; Fr: ash.

(*Fraxinus excelsior*) grew on the wood border. The honeydew collected by the colony was produced by five aphid species (*Lachnus pallipes* and *Stomaphis quercus* on oaks, *Periphyllus obscurus* on field maples, *Anoecia corni* on red dogwoods and *Prociphilus bumeliae* on the ash). Four main trails (A, B, C and D in Fig. 1) radiated from the nest, three of them running in the wood while the fourth led ants to shrubs of the wood border (for a detailed description of the nest, the network of foraging trails and the honeydew collecting sites, see Quinet and Pasteels, 1991).

Color marking

Each of the experiments started with a mass marking of foragers. The ants were marked on the gaster or the thorax with a small spot of enamel (Humbrol), without removing them from their substrate. In most experiments, the marking always concerned ants visiting aphid sites: they were marked either while running on the trunk of trees housing aphids colonies, or while collecting honeydew on aphids' colonies on shrubs. This procedure allowed us to study not only the fidelity of the foragers to the trail they use to reach the aphid site (= trail fidelity), but also their fidelity to a particular aphid site – tree or shrub – of a trail (= site fidelity).

After the marking, the ants were sampled during traffic measurements on the trails or the trunk of exploited trees, or during counts of the ants present on shrubs colonized by aphids (see below – *Trail and site fidelity*).

The reobserved marked ants will be referred as "recaptured" ants and, with few exceptions, the "recapture" period extended until no more marked ants were observed, either because they lost their mark or due to mortality. It varied from one to eight months, probably depending on factors such as the color used, the number of ants marked and the time of the season.

Trail and site fidelity

Marking experiments were realized in early spring, late spring, summer and autumn (Table 1). The ants were marked on a tree or a shrub that they visited to collect honeydew. However, in the late spring experiment (exp. 3 in Table 1), the ants did not collect honeydew on the tree where they were marked (the tree was not colonized by aphids), but sugared water (1 M). The sugared water was provided by modified water distributors for birds placed in a wooden box which was attached to the trunk of the tree, about 15 meters from the nest (Quer-B in Fig. 1). The distributors were placed on early May 1986 and were constantly supplied with sugared water until the beginning of September 1986.

After the marking period, the ants were sampled in two ways in order to study the trail fidelity (a) and the site fidelity (b):

(a) a daily measurement of the ants' traffic was realized between 3 p. m. and 5 p. m., on each of the main trail (about 1.5 M from the nest entrance), 3 to 4 times per week during periods extending generally until no more marked ants were observed. The counting time was 5 minutes for each measurement of both outward and return flow. The data used to calculate the coefficients of fidelity were those obtained from the two-way traffic (inward + toward). In the case of the ants marked in autumn, samplings were also made in the spring of the next year in order to assess the preservation of trail fidelity after the winter.

(b) traffic measurements were realized on the trunk of the tree were the ants were marked, as well as on the trunk of all the other exploited trees from the same trail. The frequency of the traffic measurements was, according to the experiment, from one to four times per week (see Table 1).

In one experiment in which only site fidelity was investigated (exp. 2 in Table 1), a different marking and sampling procedure was used: the ants were marked on a shrub, directly on aphids' colonies, while they were collecting honeydew, and instead of making traffic measurements after the marking, ants on the aphids sites were counted. The ants were marked at the end of May on a small field maple shrub reached by trail D (Fig. 1), on the wood border. Five other shrubs colonized by aphids and exploited by ants (four field maples and a dogwood) were reached by trail D. After the marking period, the ants present on the exploited shrubs of trail D were counted, once a day, 3 to 4 times per week, until the end of September, and the number of marked ants was noted separately, according to their color. However, owing to the large size of some of the shrubs, it was not possible to count the ants on them: two large field maples were not inspected while on another large field maple (ACER-D2 in Fig. 1), only two selected branches were inspected (see below). Therefore, in that experiment, our results will express the site fidelity only with regard to the inspected sites, but not to all the sites visited by ants on trail D.

Table 1. Coefficients of trail fidelity (a) and of site fidelity (b) (Co %) for ants marked on different sites from different trails, and at different periods of the season. QUER: oak; ACER: field maple; A, B, C, D: main trail reaching the marking site (see in Fig. 1). Co (Conservants): number of marked ants recaptured on the trail reaching the site where they were marked (a), or on the site itself (b). De (Deviants): number of marked ants recaptured on the other trails (a) or on the other sites which are reached by the same trail than the marking site (b). Ho (null hypothesis): theoretical % Co expected if the marked ants would distribute according to the total relative activity of the trails (a) or the sites (b)

EXP N°	Place of marking (no. of ants marked)	Date of marking	Recapture period	No. of inspec-tions	Total no. of recaptures (Co + De)	Co %	Total activity	Total relative activity (%) (Ho)	X^2 (df = 1)	P
Early spring										
1	QUER-A (2000)	23.–24.IV.86	a. 28.IV.–20.V.86	18	316	a. 57	17393	9,9	774.7	$P < 0.001$
Spring and summer										
2	ACER-D1 (500)	23.–30.V.85	b. 3.VI.–24.IX.85	52	1418	b. 90	47910	47	1096	$P < 0.001$
3	QUER-B (1300)	27.V.–11.VI.86	a. 12.VI.–24.VII.86	20	444	a. 88	28500	18	1542	$P < 0.001$
			b. 12.VI.–24.VII.86	19	353	b. 92	2832	45	360.6	$P < 0.001$
4	QUER-C (3000)	10.–13.VI.85	a. 17.VI.–12.VIII.85	28	255	a. 97	32672	44	294	$P < 0.001$
			b. 18.VI.–31.VII.85	7 (*)	104	b. 91	3490	48	80	$P < 0.001$
5	QUER-A (1100)	12.–14.VIII.85	a. 19.VIII.–4.XI.85	30	242	a. 96	21320	22	788	$P < 0.001$
			b. 20.VIII.–29.X.85	9 (*)	59	b. 85	1201	35	64	$P < 0.001$
Autumn and after winter										
6	QUER-A (6050)	2.X.–14.XI.84	a. 23.X.–26.XI.84	14	498	a. 95	5805	19	2112	$P < 0.001$
			a. 3.IV.–31.VII.85	62	961	a. 83	60820	12	4657	$P < 0.001$
			b. 16.IV.–23.VII.85	15 (*)	308	b. 85	2005	62	82	$P < 0.001$
7	QUER-C (7200)	2.X.–14.XI.84	a. 23.X.–26.XI.84	14	394	a. 99	5805	74	144	$P < 0.001$
			a. 3.IV.–16.V.85	23	71	a. 87	12678	47	45	$P < 0.001$
			b. 9.IV.–28.V.85	8 (*)	40	b. 85	2305	43	27	$P < 0.001$

* one inspection per week.

Micro-site fidelity

Concurrently with the marking described above, markings were also made on another shrub reached by trail D, a large field maple (ACER-D2 in Fig. 1), in order to investigate the foragers' fidelity to particular branches of a shrub. Two different colors were used, one to mark ants (500 specimens) on a selected branch of the shrub, the other to mark ants (1300 specimens) on the remaining branches, except on another selected branch where no marking occurred. The recapture procedure was the same as that described above.

Fidelity to hunting ground areas

In spring and summer, trails leading ants to hunting ground areas, with a lifetime of about 6 weeks, and always originating from main trails, generally from their extremities, are observed (Quinet and Pasteels, 1991).

In order to assess the foragers' fidelity to hunting ground areas, ants were marked at the end of July on three hunting trails (a different color for each trail) which had developed from an extremity of trail C (Fig. 1 and Table 3). Subsequently measurements of the ants' traffic were realized on each of the three hunting trails, about 0.4 m from their respective junction with the main trail.

Site and trail fidelity after changes in food sources distribution

In 1984 and 1985, it was observed that a branching of trail C (trail C′ in Fig. 1), terminated in a small ash colonized by the aphid *P. bumeliae*, and that this branch trail was active during only three months, from the beginning of May to the end of July when the aphids left the ash to reach their secondary host (firs of the genus *Abies* – Heie, 1980) (see Quinet and Pasteels, 1991 for more details). Since a similar development was expected in 1986, 2400 ants were marked on the ash from June 3rd to 11th in order to study the behavior of the marked ants after the desertion of the ash by the aphids. After the marking period, a daily traffic measurement was realized on each of the trails (trails A, B, C, C′ and D), 3 to 4 times per week, from June 9th to July 22nd. From the data, we have analyzed the foragers' fidelity to trail C′ inside the trail system including only trails C and C′ (Fig. 1), and their fidelity to the system (C+C′) inside the whole trail network.

Fidelity coefficients and statistical analyses

We used the fidelity coefficient defined by Rosengren (1971): % Co or $100 \times (\mathrm{Co}/\mathrm{Co}+\mathrm{De})$, where Co ("conservants") is the number of marked ants "recaptured" on the trail (or site) where they were marked (outward and return flows grouped) and De ("deviants"), the number of marked ants "recaptured" on the other trails (or sites).

For each experiment, a X^2 test was used to compare the proportion of Co observed with the proportion of Co expected if the ants had no preference for a particular trail. According to null hypothesis (Ho), the % Co should be of the same as the total relative activity (marked + unmarked – outward + return flows) observed on the marking trail (or site) compared with the total activity observed on all the trails (or sites of a trail).

Results

Trail and site fidelity

Ants marked in late spring, summer and autumn showed a significant high trail fidelity, with fidelity coefficients ranging from 88 to 95% Co (Table 1 – experiments 3a to 7a). Furthermore, ants marked in the autumn, but "recaptured" the next year also exhibited a high trail fidelity (Table 1 – exps. 6a and 7a). This latter result clearly shows that trail fidelity persists after a 5 months hibernation period, although a significant decrease in trail fidelity is observed after the winter for foragers marked in the autumn (95 and 99% Co in autumn versus 83 and 87% Co respectively after the winter – X^2 test: $p<0.001$). Foragers marked in the autumn showed fidelity to their trail up to July of the next year, after 8 months (Table 1 – exp. 6a). Trail fidelity does not fade away with time, since the trail fidelity coefficient remains fairly constant when the recapture data were analyzed for each consecutive week during periods of 1 to 5 months (Table 2), although the ants showed a more fluctuating trail fidelity with time after winter (exp. 3 – Table 2).

The trail fidelity coefficient of foragers marked in early spring is lower (57% Co, exp. 1 in Table 1) and significantly different (X^2-test: $p<0.05$) from those observed later in the season (see above), but statistically significant.

A similar degree of foragers' fidelity was observed on particular aphid sites, trees or shrub (exps. 2b to 7b – Table 1), and like trail fidelity, site fidelity is observed for long periods (up to 4 months – exp. 2 in Table 1) and is preserved through the hibernation period (exps. 6b and 7b in Table 1). This demonstrates that the foragers specialize not only on a particular trail, but also on a particular aphid-site on that trail. In the experiment 3 (Table 1), the ants were marked about 3 weeks after the placement of distributors of sucrose on the tree's trunk, the only exploited food source on that tree. It can herefore be concluded that the time required for ants to become highly specialized on a new site once discovered is at most 3 weeks.

Micro-site fidelity

In addition to site fidelity, foragers showed a strong specialization on particular branches of a shrub.

From the 70 ants originally marked on a selected branch of the field maple ACER-D2 (Fig. 1) and recaptured in a four months' period, all were found on the marking branch (100% Co, X^2 test = 152, 1 df, $p<0.001$).

Although a great number of ants (1300) were marked on the remaining branches of ACER-D2, except on another selected branch, only 8 marked ants were recaptured on the two selected branches in the same four months' period.

Table 2. Trail fidelity coefficients (Co %) during consecutive one week periods for some of the marking experiments (the number of the experiments refers to that of the experiments in Table 1). I: number of inspections. R: total number of recaptures

Week	Experiment 3 spring			Experiment 5 summer			Experiment 6 autumn			Experiment 6 after winter		
	I	*R*	Co %	*I*	*R*	Co%	*I*	*R*	Co%	*I*	*R*	Co %
1	1	33	97	3	70	100	2	130	98	2	38	89
2	4	121	88	3	37	92	3	167	93	3	98	91
3	3	84	98	/	/	/	3	95	93	4	78	91
4	3	52	73	/	/	/	3	87	95	4	103	81
5	4	70	87	4	25	96	2	18	100	2	13	85
6	3	65	85	3	26	96				4	94	73
7	3	19	89	4	40	97				4	92	75
8				4	11	91				4	70	83
9				3	10	100				4	103	83
10				3	16	93				4	88	89
11				2	4	75				3	12	67
12				1	3	100				3	21	76
13										4	22	77
14										4	41	80
15										4	30	70
16										3	27	93
17										4	27	89
18										2	4	100

Fidelity to hunting ground areas

A high foragers' specialization was also observed on particular hunting ground areas along the main foraging trails, with coefficients of fidelity ranging from 74 to 85% Co (Table 3). The differences observed between the three coefficients of fidelity are not significant (X^2 test: $p > 0.05$).

In order to examine the distribution, inside the main trails network, of the ants marked on the hunting trails, 17 measurements of the ants' traffic were made on each of the main trails (trails A, B, C and D – Fig. 1) between July 29th and August 27th. Since only the marked ants were counted, we could not make a statistical analysis of the results. Nevertheless, from a total of 219 "recaptured" marked ants, 198 (90%) were found on the main trail to which the hunting trails were connected. These results show that the hunters are as specialized on a main foraging zone (i.e., a main foraging trail) as are the honeydew collectors and that inside a main foraging zone, they specialize on particular hunting areas in the same way as the honeydew collectors on particular aphid sites. The temporary nature of the hunting trails (4 to 6 weeks) implies that the time required for ants to become specialized for the exploitation of a particular ground area is short.

Site and trail fidelity after changes in food sources distribution

The behavior of ants marked from June 3rd to 11th 1986 on a ash colonized by aphids was followed before and after the aphids left it to reach their secondary host.

The ants' activity on the trail leading to the ash (trail C′ in Fig. 1) (Fig. 2) shows a regular increase in May, a maximum activity during the first part of June (the period during which the ants were marked on the ash), and a rapid decrease followed by the end of ants' activity on that trail in July, consequently to the migration of the aphids from the ash to their secondary hosts. On the main foraging trail from which the ants departed to reach the ash (trail C in Fig. 1), the traffic remained high (from 400 to 800 ants/5 min – outward + return flows) during the major part of the season. Considering only the traffic of marked ants on trail C and its branch trail C′, it was observed that it regularly decreased on the branch trail, concurrently with the decrease of the ants' activity on that trail, while at the same time it increased on the main trail C (Fig. 3 A). The result was that the % Co values, high

Table 3. Fidelity coefficients (Co %) to hunting ground areas for ants marked on three hunting trails connected to the main trail C (see fig. 1). Co (Conservants): number of marked ants recaptured on the marking trail. De (Deviants): number of marked ants recaptured on the other trails. Ho (null hypothesis): theoretical % Co expected if the marked ants would distribute according to the total relative activity of the trails

Mark. trail (no. of ants marked)	Date of marking	Recapture period	No. of inspections	Total no. of recaptures (Co + De)	Co %	Total activity Ho	Total relative activity (%)	X^2 (df = 1)	P
I (800)	22–30.VII.86	29.VII.–3.IX.86	11	66	85	1220	45	43	$P<0.001$
II (900)	idem	idem	11	55	76	1220	41	27	$P<0.001$
III (430)	idem	idem	11	43	74	1220	14	135	$P<0.001$

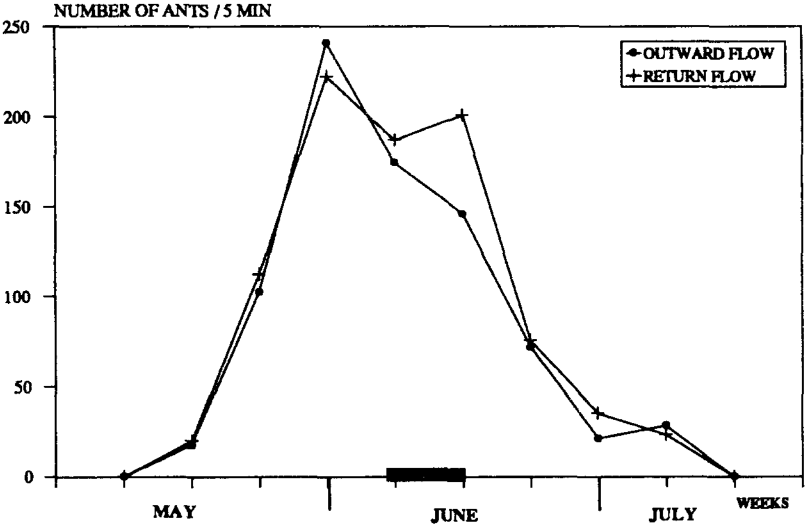

Figure 2. Ants' activity (marked + unmarked) (outward and return traffics) on the branch trail C′ (see Fig. 1). Each value is the mean of the traffic counts realized during a week. Black rectangle: period during which ants were marked on the ash (see text)

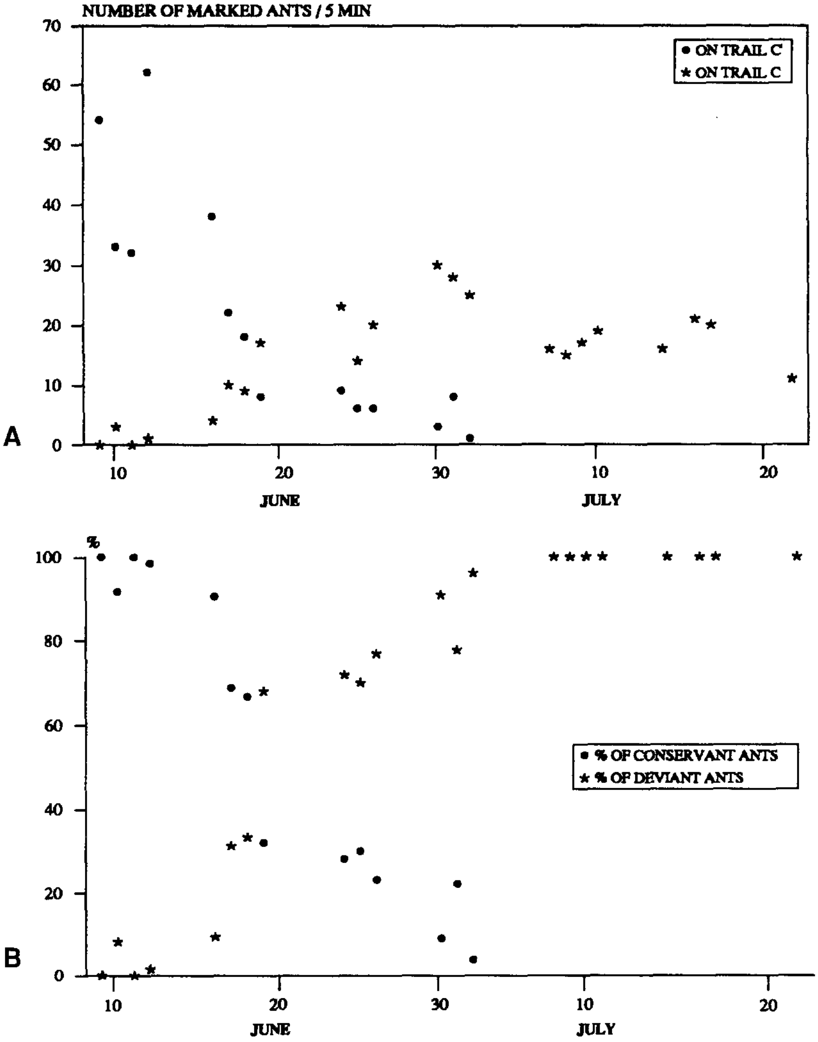

Figure 3. Trail fidelity (results of the daily inspections) of ants marked (from 3 to 11.VI.86) on the exploited ash of the branch trail C′ (see Fig. 1). **A.** Marked ants flow on trail C′ and on trail C. **B.** Percentage of marked ants "recaptured" on trail C′ (i.e. showing fidelity to trail C′) and on trail C (= deviant ants)

at the beginning of June, decreased while inversely, the proportion of marked ants "recaptured" on trail C increased and of course, reached 100% when the trail leading to the ash was no longer active (Fig. 3B).

From June 9th to July 22nd, 21 daily inspections of the main foraging trails (trails A, B, C, C′ and D – Fig. 1) were made. 677 marked ants were "recaptured", of which 619 (91%) had retained fidelity to the trail system (C + C′) (X^2 test = 268.2, 1 df, $p < 0.001$). This shows that after the disappearance of the branch trail C′ at the end of June, the marked ants remained attached to the main trail C. Furthermore, after the ash was abandoned by the aphids, observations made on the other aphid-trees reached by trail C have shown the presence of numerous ants marked originally on the ash among the foragers collecting honeydew on those trees, indicating that a redistribution of the marked ants occurs on other sites on which they probably specialize.

Discussion

The high degree of trail fidelity previously found in *L. fuliginosus* (Hennaut-Riche et al., 1980) is confirmed and it is shown that it extends to all the times of the season, except in early spring when the overall trail fidelity of the foragers is found to be lower. It is also shown that the spatial specialization is maintained for long periods (up to 4 months at least) and that along the main foraging trails, the particular aphid sites as well as the particular hunting ground areas are visited by specialized foragers. Furthermore, the foragers were found to be hyperspecialized on the particular branches of a shrub where they collect honeydew. It is demonstrated that the trail and site fidelity are retained through the hibernation period (about 5 months) and up to 4 months after the hibernation. Hennaut-Riche et al. (1980) obtained a much weaker coefficient of trail fidelity after winter (38% Co versus 83 to 87% Co in our study) but, as these authors have themselves emphasized, the small number of marked ants they "recaptured" after the winter (47 versus 961 and 71 in the present study) could explain the low trail fidelity coefficient they obtained.

These foraging patterns are very similar to those observed in the wood ants of the *F. rufa* group, and a high degree of trail constancy associated to a long-term spatial specialization of the foragers has also been reported in the North-American species *F. obscuripes* (Herbers, 1977) and *Camponotus modoc* (David and Wood, 1980; Tilles and Wood, 1986).

The main common point between all those ant species is that they have a diet mainly composed of honeydew collected regularly and in large quantities from homopterans, mainly aphids. This striking convergence between the foraging patterns of species largely relying on honeydew for their food supply supports the idea that those patterns represent an adaptation to the exploitation of food sources with a spatially stable structure (Rosengren, 1971; Carroll and Janzen, 1973; Cherix and Rosengren, 1980). Aphid colonies are characterized by a long-term life-time and by a stable location over long periods (Rosengren, 1971; Quinet and Pasteels, 1991), and it is likely that such a distribution in space and time of the main food sources has favored foraging tactics based on a learning process leading to a long-term memory (Deneubourg et al., 1986) and on the foragers' capacity to store during the winter the information about the location of food sources that they have every chance to find again in spring of the next year. Like in wood ants (*F. rufa* group), the strategy used by *L. fuliginosus* can be properly termed "predictive" (sensu Cherix and Rosengren, 1980), in that it correlates past and future rewards. In this respect, the precise restoration of the trail system in April, when the honeydew producing colonies are not yet developed (not before the first part of May) (Quinet and Pasteels, 1991), is significant. Such a strategy has some obvious advantages: by rapidly re-occupying the previous honeydew collecting sites as early as the beginning of the spring, the specialized foragers give protection to the fundatrices, a vulnerable stage of the aphid life-cycle, and therefore ensure the perpetuation of the honeydew sources. Another advantage is to allow a rapid restoration of the territory and a rapid monopolization of the previously rewarding sites after the winter, against competitors like wood ants of the *F. rufa* group (Dlussky, 1965; de Bruyn, 1978; Mabelis, 1984).

The spatial specialization of the *L. fuliginosus* foragers was found to be of rapid type (about 3 weeks at most) but also rapidly reversible since should a site becomes no longer rewarding, the foragers redistribute on other sites on which they probably specialize. The fact that this redistribution is nevertheless restricted to the sites belonging to the same main foraging trail, to which they therefore maintain their fidelity, suggests that there is hierarchy in the foragers spatial specialization: the foragers would be first specialized on a foraging zone, i.e. a main foraging trail, next on a particular site belonging to that foraging zone, and finally on a micro-site.

This ability of the specialized foragers to rapidly shift from a no more profitable site to others shows that in *L. fuliginosus*, the foraging behavior remains flexible enough to cope with changes in the food sources' distribution. Those changes can be of rapid type like the desertion of sites by aphids but also more gradual like changes of the size of the aphids' populations on the trees and shrubs through the season. Moreover, most of the main trails lead to trees or shrubs with two or even three aphid species (Quinet and Pasteels, 1991) which of course do not have an identical life-cycle and a synchronous development of their populations. As a result, adjustments of the honeydew collectors' populations to the development of the aphids' populations on those sites, i.e., shifts of foragers between the different sites, most probably occur regularly during the season. However, given the high site fidelity coefficients obtained during most parts of the season, such shifts should affect only a minor part of the foragers and/or be very gradual.

The mechanisms responsible for the long-term spatial specialization in *L. fuliginosus* have not been investigated in the present work. Nevertheless, some considerations together with what is known in wood ants (*Formica rufa* group) allow us to make hypotheses.

In wood ants, it has been shown that the main cause of the spatial fidelity is a memory of terrestrial landmarks (tree trunks, canopy patterns, position of the highest trees on the horizon,...) (Rosengren, 1971, 1977a; Rosengren and Pamilo, 1978; Henquel and Abdi, 1981; Rosengren and Fortelius, 1986; Fourcassié, 1991). In *L. fuliginosus*, a similar visual memory of terrestrial cues is most probably also the base of the foragers' spatial specialization. The persistence of a chemical trail during the winter is highly unlikely considering that the soil is washed by rains and snow. In addition, the soil is covered by a thick layer of dead leaves after the winter, and, even if chemical traces subsisted after the winter, they could explain the precise restoration of the trail network in spring, but not the retention of trail fidelity.

Rosengren (1977a and b) found strong evidence that in wood ants, the trail system constancy is determined by a true topographic tradition based on the foragers' capacity to store the topographic information about their trail during the winter and to transmit it to the next younger generation of foragers. According to Rosengren (1977a), the trail system is restored in spring by the old specialized foragers which recruit and guide the young and naïve (not specialized) foragers which will become themselves specialized on a particular trail later in the season. Our results suggest a similar topographic tradition in *L. fuliginosus*. The observed retention of the trail and site fidelity after the winter indicates that it exists a population of foragers storing the information about the trails throughout the winter. On the other hand, the lower trail fidelity coefficient observed for ants marked in early spring suggests that a part of the early spring foragers' population is composed of not specialized foragers, probably naïve and young ones, like it was observed in wood ants (Rosengren, 1977 a). The existence of such a worker force of not yet specialized foragers ready to be mobilized through recruitment processes can enable a foraging organization based on the stability of the foraging structures and behaviors to maintain an important flexibility (Rosengren, 1971; Gordon et al., 1992; Sundström, 1993). Like it was suggested in wood ants, it is probable that in *L. fuliginosus*, the observed foraging strategy is an equilibrium and an interplay between a predictive strategy and more opportunistic strategies involving the use of mass communication (Cherix and Rosengren, 1980).

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