

ANALYSIS OF THE SPATIO-TEMPORAL NICHE OF FORAGING GRASSLAND ANTS IN THE FIELD

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SUMMARY

The foraging activities of four genera (six species) of grassland ants (*Formica rufibarbis*, *Tapinoma erraticum*, *Myrmica schenki*, *M. sabuleti*, *Tetramorium caespitum* and *T. impurum*) were observed in June-July 1985 at Treignes (Belgium).

Foraging activity was assessed by taking sequential records of foragers' fluxes during 30 seconds through the perimeter of 0.5 × 0.5 m adjacent field quadrats. The ants' velocities were also measured in the field; knowing their fluxes, it was possible to calculate the densities of foragers. The latter were mapped and studied as a function of climatic parameters, to understand the niche relationships of these ants.

Regarding their diurnal spatio-temporal foraging activities, the four genera were found to occupy well separated realized niches.

RESUME

Analyse de la niche spatio-temporelle de fourmis en prairie

L'activité d'affouragement de 4 genres (6 espèces) de fourmis de prairie (*Formica rufibarbis*, *Tapinoma erraticum*, *Myrmica schenki*, *M. sabuleti*, *Tetramorium caespitum* et *T. impurum*) a été observée au cours des mois de juin-juillet 1985 à Treignes (Belgique).

L'activité des fourrageuses sur le terrain est estimée par des observations séquentielles de flux d'ouvrières pendant 30 secondes à travers le périmètre de quadrats de 0,5 × 0,5 m. Les vitesses de déplacement des fourmis sur le terrain ayant aussi été mesurées, les flux sont transformés en densités de fourrageuses. Ces dernières sont cartographiées et étudiées en fonction de paramètres climatiques. Elles sont ensuite soumises à une analyse des niches écologiques.

Les quatre genres étudiés occupent des niches réalisées qui apparaissent bien séparées sur la seule base de la répartition spatio-temporelle de leur activité diurne d'affouragement.

INTRODUCTION

Niche studies are scarce in insects compared to vertebrates (e.g. LOREAU, 1986). In social insects, most studies deal with habitat rather than niche as defined by WHITTAKER *et al.* (1973); see e.g. CULVER (1972, 1974).

This work, albeit uncomplete, attempts to fill this gap in studies of social insects' foraging. It limits its scope to separation of niches through diurnal and spatial partitioning of the foraging field by an ant community according to the climatic parameters.

Most habitat and niche studies in ants were concerned with species that are of a relatively large size and forage on bare soils. This is the case for large forest Ponerinae such as *Neoponera apicalis* (FRESNEAU, 1985), for Attinae (*Acromyrmex crassispinus*, FOWLER, 1979), for Dorylinae (*Eciton burchelli*, FRANKS, 1985), for forest Formicinae (*Formica rufa*, ROSENGREN, 1977a and 1977b), and even the smaller but conspicuous *Lasius fuliginosus* (HENNAUT-RICHE *et al.*, 1980). It is also the case for desert ants such as *Cataglyphis* spp, which have been studied extensively in the field (WEHNER *et al.*, 1983), and for communities of seed-eating ants (DAVIDSON, 1977).

Such information is in comparison very scarce for grassland ants, whose foraging and recruitment behaviours are best known from laboratory studies. Some of these (*Myrmica* spp. CAMMAERTS and CAMMAERTS, 1980, *Tetramoniium* spp, VERHAEGHE, 1982 and *Tapinoma erraticum*, VERHAEGHE *et al.*, 1980) have been studied in the lab for several years. Therefore, it is especially interesting to supplement our knowledge of these species by field studies. We thus set out an experiment to record their foraging activity in the field.

MATERIAL AND METHODS

Observation of the ants

The experiments were carried out at our field laboratory at Treignes, in the southern part of Belgium (latitude : 50° 10' N, longitude : 4° 60' E, altitude : 140 m).

To facilitate the observations, we chose an area with mixed short grasses and dark sand. A square of 4.5 × 4.5 m was divided into 81 quadrats of 0.5 × 0.5 m (*fig. 1*) by white strips (3 cm broad). These strips were made in the field by the application of several coats of white enamel paint on the dark sandy soil or on the locally mowed grasses. In this way, foraging ants were obliged to cross over these strips and became clearly visible for a few seconds. Once dried completely, we did not notice any repellent effect of this device on the walking direction of the ants.

Observations were made in a sequential way (*fig. 1*). At least two people counted the ants crossing the strips of one quadrat during 30 seconds, noting the genus, which strip was crossed and towards which direction. After 30 seconds of rest, observations started again on a next quadrat. Timing was given by a magnetic tape recorder. The whole area was thus observed in two sessions of 25 and 16 minutes, giving a survey of the 4.5 × 4.5 m square in about 3/4 of an hour. The results are given for the period June-July 1985.

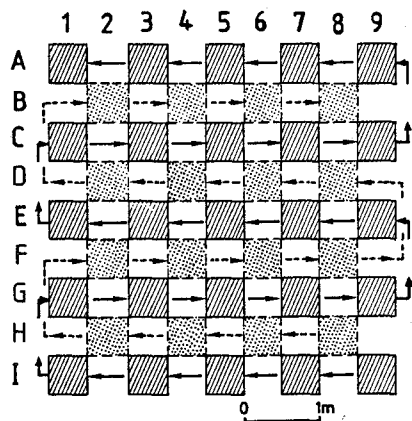


Fig. 1. — The observation area.

The large square (4.5 m × 4.5 m) is divided by a 9 × 9 grid which delimits 81 small quadrats (0.5 m × 0.5 m). The first session of observations concerns the striped quadrats and begins at the quadrat I9 to end at the quadrat A1. The black arrows show the sequence of the observations. The whole session lasts 25 minutes. The second session of observations concerns the dotted quadrats and begins at the quadrat H8 to end at the quadrat B8. The dashed arrows show the sequence of the observations. The whole session is thus completed in 16 minutes. A complete survey of the large square is achieved by consecutively performing both sessions.

Fig. 1. — L'aire d'observation.

Le grand carré (4,5 m × 4,5 m) est divisé par une grille qui délimite 81 quadrats (0,5 m × 0,5 m). La première série d'observations porte sur les quadrats hachurés et commence au quadrat I9 pour se terminer au quadrat A1. Les flèches pleines montrent la séquence des observations. Une série complète d'observations dure 25 minutes. La seconde série d'observations porte sur les quadrats pointillés et commence au quadrat H8 pour se terminer au quadrat B8. Les flèches pointillées montrent la séquence des observations. Une série complète d'observations dure 16 minutes. Un relevé complet du grand carré implique la réalisation successive des deux séries d'observations.

Measurement of ant velocity

On the same area, we measured the velocity of the foraging ants by means of a glass plate fixed 10 cm above the soil level and an aperture sight (5 mm in diameter) 40 cm above the glass plate. Looking through the sight while following an ant, its trajectory was drawn on the glass plate during a known time (*fig. 2*); timing was provided again by the magnetic tape recorder.

The length of the trajectory was subsequently measured and multiplied by 1.25 in order to obtain the actual walked distance during a known time lapse. The hour, soil temperature and genus of the ant were noted. It was thus possible to establish the correlation between speed and soil temperature for each genus.

Estimation of the number of foragers

Knowing the fluxes of ants over the strips and their actual speed, we calculated the numbers of foragers in a quadrat using a simple model:

$$F = N * P(v)$$

where: F is the exit flux from a quadrat,

N is the number of ants in the quadrat,

P is the probability for an ant to leave the quadrat and is assumed to be a function of v, its speed.

This linear model is based on the hypotheses that: (1) there are no interactions between ants and (2) the system is in a stationary state. In fact, there are interactions between ants but very few, owing to the low density of foraging ants; we thus considered

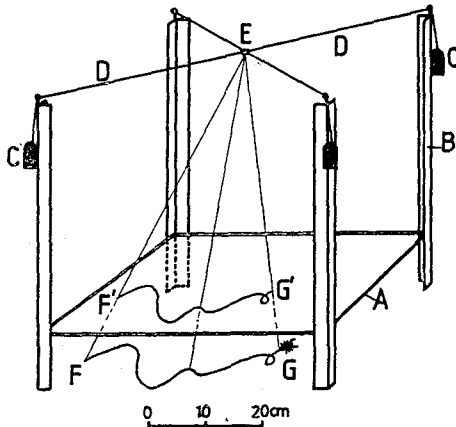


Fig. 2. — The device used to record the trajectories and velocities of ants.

A : glass plate - B : frame - C : counterweight used to straighten the string D - D : string supporting the aperture sight - E : aperture sight - F-G : trajectory of the ant - F'-G' : projection of the trajectory of the ant on the glass plate A.

Fig. 2. — L'appareil permettant d'enregistrer les trajectoires et vitesses de déplacement des fourmis.

A : plaque de verre - B : châssis - C : contrepoids destiné à tendre les câbles D - D : câbles supportant l'ocillon - E : ocillon de visée - F-G : trajectoire de la fourmi - F'-G' : projection de la trajectoire de la fourmi sur la plaque de verre A.

their effect as insignificant. Also, the system is not in a true stationary state but each of our observation sessions lasted less than 45 minutes; in such a period of time, the system may reasonably be considered as being in a stationary state.

The probability to leave a quadrat as a function of ant speed was investigated using a Monte-Carlo simulation. This showed that:

(1) The sinuosity of the ant's trajectory has no effect on the probability to leave the quadrat provided it lies under a certain limit. The sinuosities recorded from the trajectories of the studied foragers were always under this limit.

(2) There is a linear relationship between the probability to leave the quadrat and the speed of the ant for velocities lower than 2 cm/s. Beyond this point, this probability is equal to 1, that is to say, the exit flux is equal to the number of ants present in the quadrat.

Timing of observations and climatic measurements

Observation sessions were set out regularly between 8 a.m. and 8 p.m. (legal time) and occasionally between sunrise and 8 a.m. and between 8 p.m. and sunset. Night activity was not investigated. (N.B. : solar time = legal time - 1 h 45 min.).

The following climatic conditions were simultaneously recorded :

- incident light intensity, which was measured by a luxmeter whose cell was placed horizontally at soil level ;
- air temperature 10 cm above the soil level ;
- temperature at the soil level on dark sand ;
- temperature at the soil level on short grass ;
- temperature under a schistous slate 1.5 cm thick ;
- soil temperature at -5 cm ;
- soil temperature at -10 cm ;

— soil temperature at —20 cm (all temperatures were measured by a multichannel thermistor thermometer whose sensors remained in the same places during the whole study);

— air humidity 10 cm above the soil level which was measured with a psychrometer and converted into deficit of absolute humidity which accounts best for evaporation intensity.

Niche measurements

We used the niche concept defined by WHITTAKER *et al.* (1973). Niche breadth and overlap were measured using LEVINS' (1968) indices:

$$B'_i = \frac{1}{k \sum_h p_{ih}^2} \quad (\text{relative breadth})$$

$$\alpha_{ij} = \frac{\sum_h p_{ih} * p_{jh}}{\sum_h p_{ih}^2} \quad (\text{overlap})$$

Where: k is the number of quadrats or hours.

p_{ih} and p_{jh} are the proportions of foraging ants of species i and j present in quadrat h of our 4.5 × 4.5 m square (spatial distribution) or at hour h of the day (temporal distribution).

These indices were chosen because they have both the advantage of simplicity (see discussion in ABRAMS, 1980) and the interesting property that multidimensional estimates of niche breadths and overlaps can be obtained by simply multiplying the corresponding 1-dimensional estimates, provided niche dimensions are independant (MAY, 1975). This procedure was used to calculate 2-dimensional estimates.

RESULTS

The species nesting in the observation square were *Formica rufibarbis*, *Tapinoma erraticum*, *Tetramorium caespitum*, *Tetramorium impurum*, *Myrmica sabuleti* and *Myrmica schenki*. *Formica fusca*, *Lasius flavus* and *Leptothorax* sp were very scarce and recorded only occasionally (they nested outside the square); accordingly, they were not taken into account.

Although there was only one species of either *Formica* or *Tapinoma*, our work only considered genera because it was too difficult to distinguish the species of *Tetramorium* and of *Myrmica* in the field.

Climatic influences

Formica rufibarbis was active between 10 a. m. and 6 p. m., the warmest hours of the day; its optimal foraging conditions were 20,000 - 30,000 lux, 35-40° C on the soil and 3-4.5 mbar humidity deficit but it tolerated 50° C and 6 mbar of humidity deficit (fig. 3A).

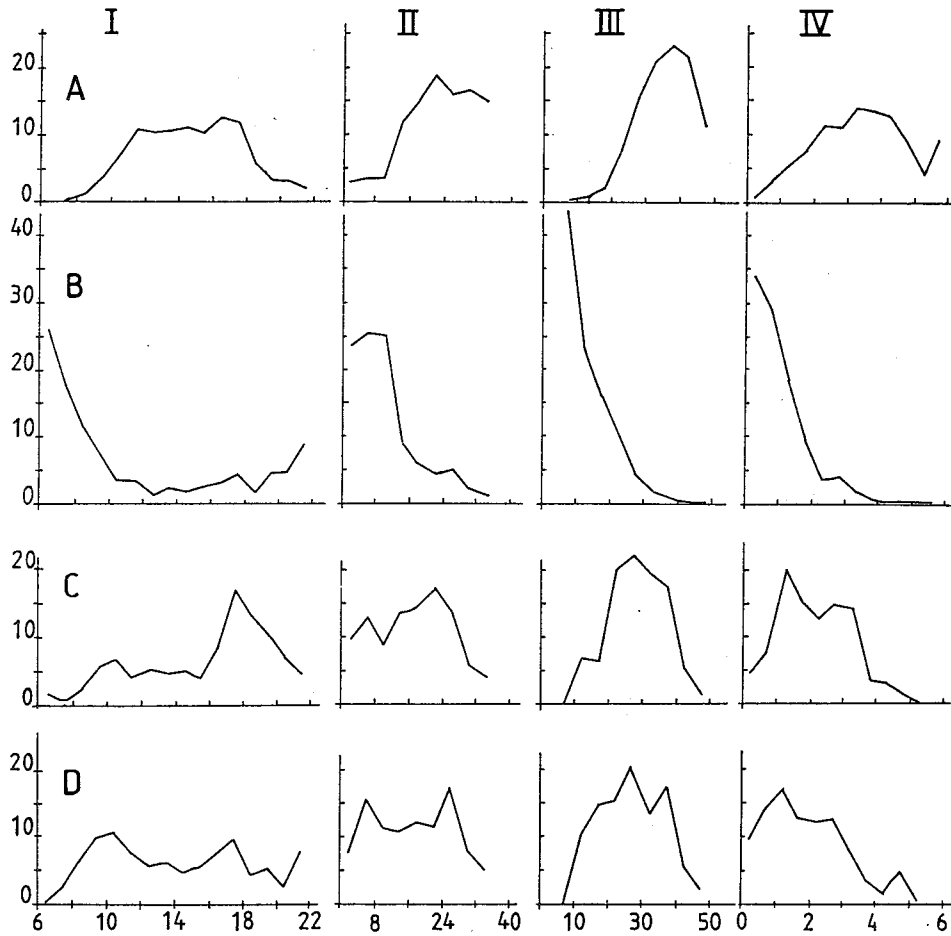


Fig. 3. — Activity of foragers and climatic influences

3A. *Formica rufibarbis*

3B. *Myrmica schenki* and *M. sabuleti*

3C. *Tetramorium caespitum* and *T. impurum*

3D. *Tapinoma erraticum*

Ordinate : for all figures,

$$Y = \frac{Y_i / N_i}{\sum_{i=1}^n Y_i / N_i}$$

where Y_i represents the number of ants observed on the whole observation area at the value i of the abscissa parameter, and N_i is the number of observations performed at this same value.

Abscissa :

I : hour, local solar time (= legal time - 1 h 45)

II : incident light intensity (in lux $\times 10^3$)

III : temperature at the soil level (in $^{\circ}\text{C}$)

IV : deficit of absolute humidity (in mbar).

Myrmica schenki and *M. sabuleti* showed the opposite tendency, being active between 6 and 9 a. m. and at sunset, with a light intensity of less than 10,000 lux; they avoided temperatures above 25° C and humidity deficits higher than 1 mbar (fig. 3B). They were probably still active during part of the night, but this was not investigated.

Tapinoma erraticum, *Tetramorium caespitum* and *T. impurum* were active almost all over the daytime, starting at 6 a. m. and stopping at 10 p. m. Their optimal climatic conditions seemed to be 20,000 lux, 25-30° C and 1-3 mbar humidity deficit. They avoided both low and high temperatures and humidities (fig. 3C, 3D).

Spatial distributions

The overall mean densities of foragers over the entire period June-July 1985, the whole area and all 251 observation sessions, amounted to:

<i>Formica</i> :	3.0 ind/m ²
<i>Myrmica</i> :	0.5 ind/m ²
<i>Tetramorium</i> :	0.7 ind/m ²
<i>Tapinoma</i> :	1.0 ind/m ²

The figure for *Myrmica* is underestimated since nocturnal and very early morning activity were not taken into account.

Maps of iso-foraging densities were drawn using a computer program.

In *Formica*, we can guess the presence of two main but diffuse tracks. A decreasing gradient from the nest entrance spread over an area much larger than the study area (fig. 4A).

Fig. 3. — Activité des fourrageuses et influences climatiques

- 3A. *Formica rufibarbis*
 3B. *Myrmica schenki* et *M. sabuleti*
 3C. *Tetramorium caespitum* et *T. impurum*
 3D. *Tapinoma erraticum*

Ordonnée : pour les quatre figures,

$$Y = \frac{Y_i / N_i}{\sum_{i=1}^n Y_i / N_i}$$

où Y_i représente le nombre de fourmis observées sur la totalité de l'aire d'observation à la valeur i du paramètre de l'abscisse et N_i le nombre d'observations réalisées à cette même valeur.

Abscisses :

- I : heure solaire locale (= heure d'été - 1 h 45)
 II : lumière incidente (en lux $\times 10^3$)
 III : température au niveau du sol (en °C)
 IV : déficit d'humidité absolue (en mbar).

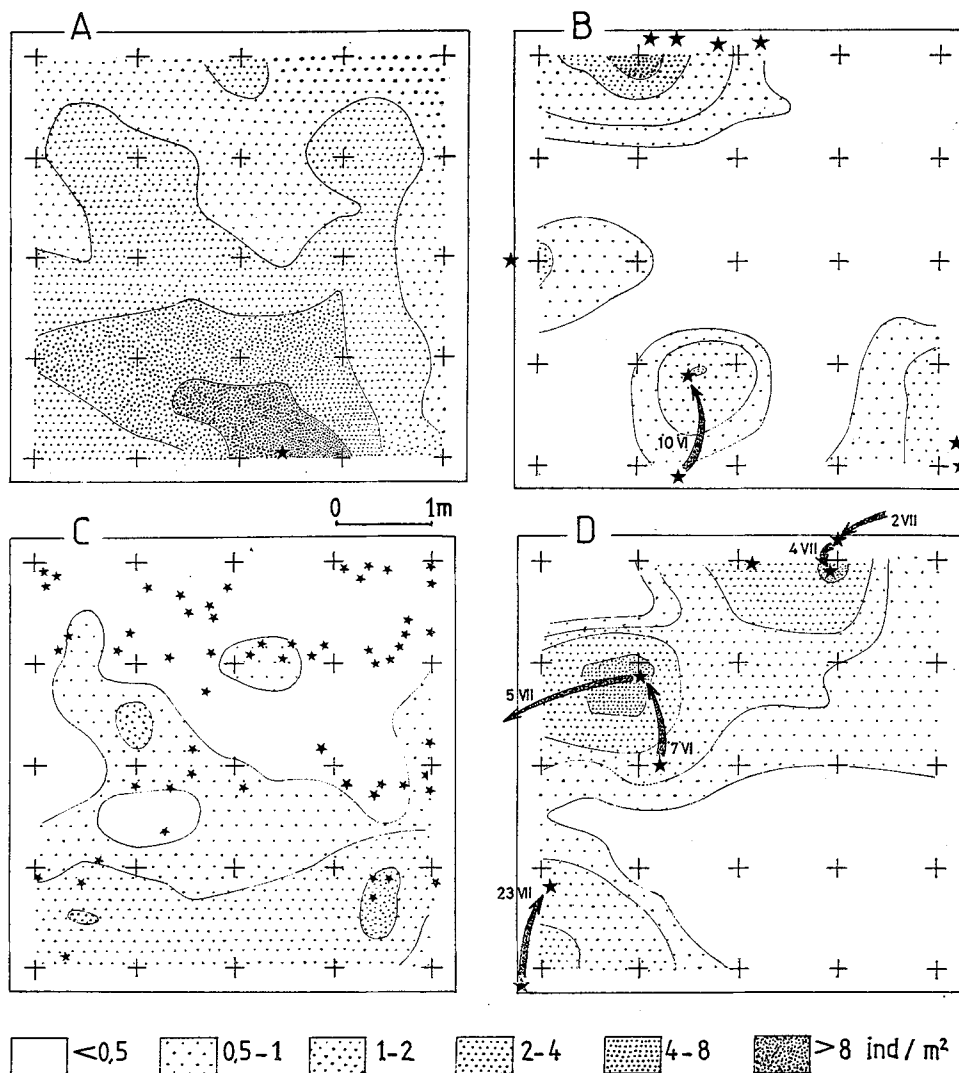


Fig. 4. — Spatial distribution of foraging activity

- 4A. *Formica rufibarbis*
 4B. *Myrmica schenki* and *M. sabuleti*
 4C. *Tetramorium caespitum* and *T. impurum*
 4D. *Tapinoma erraticum*

The isodensity curves represent the mean densities (number of foragers/m²) recorded over the whole observation period (June-July 1985).

The location of each nest entrance is represented by a star and their movings by arrows. Movings dates are mentioned: e.g. 2 VII means that it occurred on the 2d day of July.

Fig. 4. — Répartition spatiale de l'affouragement

- 4A. *Formica rufibarbis*
 4B. *Myrmica* et *M. sabuleti*
 4C. *Tetramorium caespitum* et *T. impurum*
 4D. *Tapinoma erraticum*

Les courbes d'isodensités représentent les densités moyennes (en nombre de fourrageuses/m²) observées pendant toute la période d'observation (juin-juillet 1985). Les sorties de nid sont symbolisées par des étoiles et leurs déménagements par des flèches. Les dates des déménagements sont indiquées: par exemple 2 VII signifie qu'il s'est déroulé le 2 juillet.

In *Myrmica* and *Tapinoma*, activity densities looked like small hills clearly centered on the nests with a radius of 1-1.5 m in both cases (*fig. 4B and 4D*). *Tapinoma* however was characterized by frequent nest movings. During the two months of observations, we recorded 5 movings involving 3 nests, so that the "hills" of foraging were limited in time. The dates of moving are mentioned on the map (*fig. 4D*).

The foraging distribution of *Tetramorium* was clearly different from that of the previous 3 genera: its activity density was spread over the whole study area. The nest entrances were numerous and rather short-lived. The foragers used shallow subterranean paths, in this way limiting the distances they had to walk on the soil surface. This explains that the mean density of foragers was rather low on the soil surface (0.7 individual/m²) and that the lowest activity density was observed in the region where nest entrances were most numerous (*fig. 4C*). In this region, their main traffic probably occurred in their shallow gallery net. But even so, *Tetramorium* was very efficient in discovering food sources.

Niche measurements

Let us emphasize in our analysis of niche breadth and overlap that the measurements only concerned foraging workers and there were no measurements made at night.

Table I provides the data concerning the temporal distribution of foragers. *Myrmica* species showed the narrowest niche, suggesting that they

Table I. — Temporal distribution of foraging activity: niche overlaps and breadths. *

Tableau I. — Distribution temporelle de l'activité d'affouragement: recouvrements et largeurs des niches.

Species j Species i	Overlaps α_{ij}				Means α_i	B'_i Relative breadth
	<i>/Formica</i>	<i>/Myrmica</i>	<i>/Tetra- morium</i>	<i>/Tapinoma</i>		
<i>Formica/</i>		0.32	0.79	0.75	0.62	0.67
<i>Myrmica/</i>	0.23		0.32	0.38	0.31	0.49
<i>Tetramorium/</i>	0.82	0.46		0.78	0.69	0.70
<i>Tapinoma/</i>	0.95	0.65	0.94		0.85	0.85
Mean α_j	0.67	0.48	0.68	0.64		

* The coefficients are given for the overlap by species i's niche on species j's niche. For example, *Tapinoma's* niche overlaps *Formica's* niche with a coefficient of 0.95 and is overlapped by the latter with a coefficient of 0.75.

are the most specialized ants with respect to the period of the day when they forage actively. However this relative breadth is probably underestimated since these ants forage also during part of nighttime (DELALANDE, 1986).

All the lowest overlaps (< 0.5) occurred with the *Myrmica* species. Furthermore, these overlaps are overestimated because of the lack of observations at night. It is interesting to notice that *Myrmica* is intermedate in size between *Formica* and the other two genera. On the other hand, the two highest overlaps (> 0.9) occurred with *T. erraticum*.

Table II provides the data concerning the spatial distribution of foragers. Both *Myrmica* spp and *T. erraticum* had narrow niches and low overlaps. The overlaps with *T. erraticum* were especially low (all but one are < 0.5). This can be explained by the peculiar behaviour of approaching/appropriating food of this species: it literally creeps into available spaces, having only access to the food sources in the absence of other ant species and fleeing when another ant approaches. The nest-moving habits of *T. erraticum* probably complete this behaviour, enabling it to exploit the temporarily vacant spaces.

Table II. — Spatial distribution of foraging activity: niche overlaps and breadths. *

Tableau II. — Distribution spatiale de l'activité d'affouragement: recouvrements et largeurs des niches.

Species j Species i	Overlaps α_{ij}				Means $\alpha_{.j}$	B' _i
	/Formica	/Myrmica	/Tetramorium	/Tapinoma		Relative breadth
Formica/		0.65	0.79	0.49	0.64	0.65
Myrmica/	0.43		0.41	0.33	0.39	0.43
Tetramorium/	0.77	0.60		0.59	0.65	0.64
Tapinoma/	0.34	0.35	0.42		0.37	0.46
Mean $\alpha_{.j}$	0.52	0.54	0.54	0.49		

* See table I.

Finally table III summarizes the data concerning the spatio-temporal distribution of foraging workers. Most 2-dimensional overlaps were very low. It is interesting to note that the highest overlaps occurred between *F. rufibarbis* and *Tetramorium* spp, two genera which are very different in size and ignore each other, at least while foraging individually. The small *Tetramorium* can be seen foraging in the refuses and close to the entrance of the nest of *F. rufibarbis*.

Table III. — Spatio-temporal distribution of foraging activity: niche overlaps and breadths. *

Tableau III. — Distribution spatio-temporelle de l'activité d'affouragement: recouvrements et largeurs des niches.

Species j Species i	Overlaps α_{ij}				Means α_i	B' _i Relative breadth
	/Formica	/Myrmica	/Tetra- morium	/Tapinoma		
Formica/		0.21	0.62	0.37	0.40	0.44
Myrmica/	0.10		0.13	0.13	0.12	0.21
Tetramorium/	0.63	0.28		0.46	0.46	0.45
Tapinoma/	0.32	0.23	0.39		0.31	0.39
Mean α_j	0.35	0.24	0.38	0.32		

* See table I.

DISCUSSION

On account of the social structures of ants, measuring the ecological niche in their case is both easier and more complicated than in the case of solitary insects. It is easier because of the existence of permanent nests and therefore, of their central place foraging. It is more complicated because of the social aspects of their foraging strategies.

The existence of permanent nests allows mapping of space occupation. However this mapping is not always easy because on the one hand the nests of some species are polydomic and on the other hand, many species move their nests from time to time (HERBERS, 1985); some species such as *Tapinoma erraticum* move rather frequently (five migrations by three colonies in our two month observations). Obviously, nest mobility should be considered as a niche component but was not included here.

Territorial behaviour is frequent in ants and is accompanied by contest competition: heavy fightings occur between nests of *T. caespitum* and *T. impurum* (ROISIN, 1982). This behaviour results in a clear spatial separation between nests.

The foraging strategy may disturb the relation between size of the prey and size of the predator, one of the classical dimensions used in niche studies. The relation between ant size and prey size was emphasized by HANSEN (1978), CHEW and DE VITA, 1979 (in EASTLAKE and CHEW, 1980) and WEHNER *et al.* (1983). TRANIELLO (1987) also found a significant correlation between worker size and prey size when the foragers act individually, but smaller

ants retrieve a larger percentage of their food cooperatively than do larger ants.

In the case of *F. rufibarbis*, the largest species in our study, foraging ants capture prey and bring them back to the nest individually. These prey may be as large as the foraging ant. In the two small *Tetramorium* species, foraging ants are also able to capture and bring back small prey individually. But if they encounter large food sources, they recruit other workers and are able to handle much larger prey than is *F. rufibarbis*. Our observations thus confirm the equivocal relation between prey size and ant size. In spite of this, we have put the species in a decreasing order of size in *tables I, II and III*.

The way foragers succeed in appropriating food sources is an important element of the competition between species. *F. rufibarbis* often approaches the food source in an aggressive and abrupt way which frequently makes other ants run away. *Tetramorium* and *Myrmica* species recruit nestmates to the large food sources. We observed that such a behaviour allows an effective defense of the discovered item; these observations confirm those of MABELIS (1984). *T. erraticum* approaches the food source in a completely different way, collecting food rapidly and only if no other ant is present on the food source. This species carefully avoids aggressive contacts with other species, and quits immediately the food source when another ant species approaches. Its behaviour is however completely different in close vicinity of its nest: in this case, it chases away other ants (even the large *Formica*), probably by using its chemical defenses.

Our niche measurements for the spatial dimension should be very sensitive to local conditions, because occupation of space seems strongly influenced by direct interference between species. In this case, the realized niche of a species may be very different from its fundamental niche, and it is difficult to draw firm conclusions about the potential for coexistence between the species studied. However, since we consciously chose the study site so as to include the nests of as many genera as possible (*Formica rufibarbis* nests are scarce), we may at least confidently state that we did not overestimate the separation between the species' realized niches.

As a conclusion, it appears that the foraging niches of the ant genera we studied are clearly separated on a spatio-temporal basis. This is congruent with the works of DELALANDE (1986) and MABELIS (1984). Obviously, our foraging niche analysis is not complete since we have not estimated the fundamental dimension of the diet, which might separate the ants' niches even better. Such a conclusion contrasts with the fact that a superficial observation may lead to the impression that most of these sympatric ant species are foraging together everywhere and at any time of the day. This conclusion, that we have reached at the level of the genera, is very likely to be also valid for the species since the two species of *Myrmica* are completely separated in space and so are the nests of the two species of *Tetramorium*.

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