Habitat exploitation and intercolonial relationships in the ant *Cataglyphis cursor* (Hymenoptera : Formicidae)

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ABSTRACT

Cataglyphis cursor is a subterranean nesting ant species distributed randomly in favourable sites (flat and arid places in Mediterranean region). It is a scavenger, showing individual foraging without recruitment. Individuals of various colonies can feed peacefully on the same food source, for example a droplet of sugar water, but they generally feed on small prey transported into the nest. These ants do not have territories: neither the exploited areas nor the entrances to the nest are defended against workers of neighbouring colonies. Colony foraging areas overlap considerably. The activity is strictly diurnal with an activity peak varying according to the season. Three other species are studied for comparison.

KEY WORDS: Formicidae, *Cataglyphis*, daily activity, competition, distribution, exploitation of the habitat, foraging area.

RÉSUMÉ

Cataglyphis cursor est une fourmi qui a été étudiée principalement en laboratoire car elle se reproduit par parthénogenèse thélytoque. Nous avons entrepris son étude sur le terrain dans la région méditerranéenne. C'est une espèce terricole dont les nids sont distribués selon une loi normale dans les sites favorables (endroits plats avec une faible végétation). Elle est nécrophage et les ouvrières fourragent individuellement, il n'y a pas de recrutement. Des individus de diverses colonies peuvent se nourrir pacifiquement sur une même source de nourriture, par exemple une goutte d'eau sucrée, mais récoltent plutôt des cadavres d'insectes de petite taille. Il n'y a pas de territoire ; le domaine vital et même l'entrée du nid ne sont pas défendus contre les ouvrières des colonies voisines. Ainsi les aires de récolte des colonies se chevauchent considérablement. Cette structure de population originale pour des insectes sociaux est discutée en relation avec les fondations par bouturage que l'on observe chez cette espèce. Ces fourmis sont strictement diurnes, mais le pic d'activité observé aux heures chaudes de la journée varie selon les saisons. Trois autres espèces (*Messor structor, Camponotus aethiops* et *Pheidole pallidula*) sont étudiées à titre de comparaison.

INTRODUCTION

Cataglyphis cursor (Fonscolombe, 1846) is a Mediterranean formicine ant species living in dry, arid and unshaded habitats with sparse vegetation (BERNARD,

1968, 1983; CAGNIANT, 1976 a). It is also found in some areas where vegetation is quite abundant, for example in Provence (LENOIR *et al.*, 1988) and in the Barcelona region (CERDA *et al.*, 1989). CAGNIANT (1976 b) indicated that *C. cursor* societies are monogynous and monodomous, which was confirmed by LENOIR *et al.* (1988). A previously unknown mode of founding new colonies was discovered (*ibid.*): *C. cursor* disseminates by budding. Colony fission occurs after mating of sexuals: the males fly off from their natal nest, but females do not leave and remain near the nest entrance where they are fertilised during a nuptial course. Females then reenter their natal nest. There is a short period during which colonies can be polygynous. During the days following this period a group of workers can move with brood, callow workers and a newly inseminated queen to a new nest site. If such budding does not occur, supernumerary queens within the colony are rejected. For these reasons, species propagation is limited to short distances, and colonies within the same habitat are related. This explains why few aggressive behaviours are observed between individuals of different colonies in the same location (NOWBA-HARI & LENOIR, 1984). Workers placed on the entrance of an alien neighbouring colony are frequently tolerated and can enter the alien nest, where they may be adopted (LENOIR *et al.*, 1988).

In this paper we present data concerning the use of habitat in *C. cursor*. Firstly diel activity was observed and permitted to experiment during the favourable periods. Secondly, to study habitat exploitation, it was necessary to locate all the nests and have an estimation of the nest density. Later, experiments were conducted on foraging activity and intercolonial relationships. In some cases information on three species is given for comparison.

MATERIALS AND METHODS

All observations were made in July and August 1985 and 1986 in two places in France: near Apt (Vaucluse, 500 m altitude) and near Le Muy (Var, 150-200 m). Nest entrances were noted with a numbered label on 1 m × 1 m quadrats. When necessary, workers were captured and marked with a dot of "Céramique à froid" paint, and released 5 or 10 minutes later. This technique was tested in the laboratory, where the marked ants immediately reentered their nest without hostility from their nestmates, and did not present higher mortality over the following weeks. All observations were made during the daytime from 8 to 16 h (TU) which coincides with the activity period of these ants.

The distribution of the two populations was studied using the nearest neighbour distance measure, according to the method proposed by CLARK & EVANS (1954). This method is suitable here because colonies have single entrances to their nest. The distribution index R can range from 0 (perfect aggregation) to 2.1491 (perfect hexagonal distribution). A value of 1 indicates a random distribution.

A device for automatically recording the activity of ants in natural conditions was used by DELALANDE (1985, 1986) to study some Mediterranean species, including *C. cursor*. Boxes were bored with a hole, and fitted with a photoelectric cell. The box was used to form a tunnel through which the ants must pass. The cell is connected to an automatic graphic recorder, which records the total traffic of ants leaving or entering the box. Boxes were placed either on the nest entrance, giving an estimate of the activity of the nest (for *Cataglyphis cursor* and *Camponotus aethiops*), or on the surface of the soil with food sources. Seeds were offered to *Messor*, egg yolk to the omnivorous *Pheidole pallidula*. As *C. cursor* workers forage individually (see below) this method was not suitable for recording the activity on food sources for this species. Data were obtained near Apt (July 1984 and May 1985), and are the means for 3 days of recording.

We did not make further studies of the diet of *C. cursor*. It is well known that all species of *Cataglyphis* are necrophagous and prefer to eat dead arthropods (DELYE, 1968; HARKNESS & WEHNER, 1977; WEHNER *et al.*, 1983; RETANA *et al.*, 1986; CERDA *et al.*, 1989). TOHMÉ and TOHMÉ (1982) observed a poor efficiency in predation on live caterpillars by *Cataglyphis* in Lebanon. In *C. cursor* vegetable products represent 10% of the retrieved items, but seeds without elaiosome are ignored. From the point of view of ants elaiosomes are analogous to insect corpses. This result is not a sign of granivory (RETANA, pers. comm.). Among animal preys, 50% are dead ants (RETANA *et al.*, 1986). The proportion of workers that go back to the nest with a solid item is relatively low (13-27%) and unloaded ants frequently have nectar in their crop, as observed by WEHNER *et al.* (1983) for *C. bicolor* and RETANA *et al.* (1986) for *C. cursor*. These authors consider that 60% of unloaded workers are nectar transporters in *C. cursor*. The origin of nectar is not known: RETANA *et al.* (1986) indicated that it was very rare to observe *C. cursor* licking plants. HERRERA *et al.* (1984) sometimes observed this behaviour in *Cataglyphis viatica*. DU MERLE (1982) reported that *C. cursor* is sometimes captured on trees during beatings and STARY *et al.* (1988) observed *Cataglyphis* tending aphids in some shrubs and plants. An important part of liquid food might also be haemolymph of large prey which is licked by the ants (see experiment 4). The analysis of loads retrieved by the foragers shows that species appear to be selective with respect to food size: small species frequently collect dead ants whereas larger species (such as *C. cursor*) retrieve dead isopods in large numbers (SCHMID-HEMPEL, 1987).

RESULTS

DAILY ACTIVITY

To study the activity rhythm two methods were used: (i) counting the traffic at the nest entrance for 5 minutes every half hour, and (ii) automatic activity
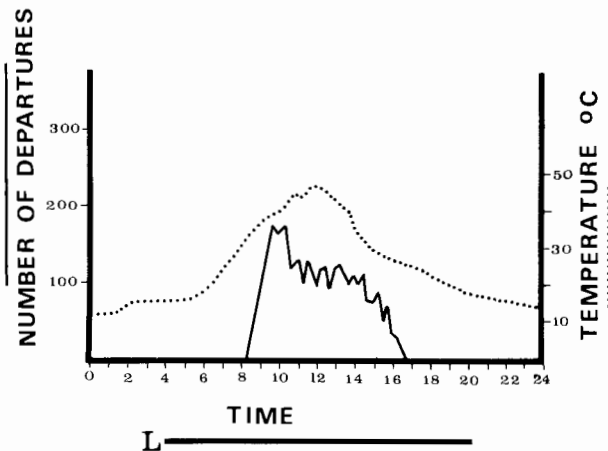

FIG. 1. — Activity rhythm: traffic (exits) for one nest sampled 5 minutes by visual counting every half hour from 8 to 18 hours (July 1983). Data are means for three consecutive days. Time is solar time.

recording. Figure 1 shows the rythm of one colony with visual counting in July 1984. A diurnal activity appears. In the morning, when temperature increases, a few workers free the nest entrance which is closed during the night with sand and

small stones, and foragers begin to leave the nest. The highest level of activity occurs during the hottest hours when numerous workers make only a brief exit and reenter the nest. They are not counted here because they are not foragers. There is a progressive decrease of activity in the evening.
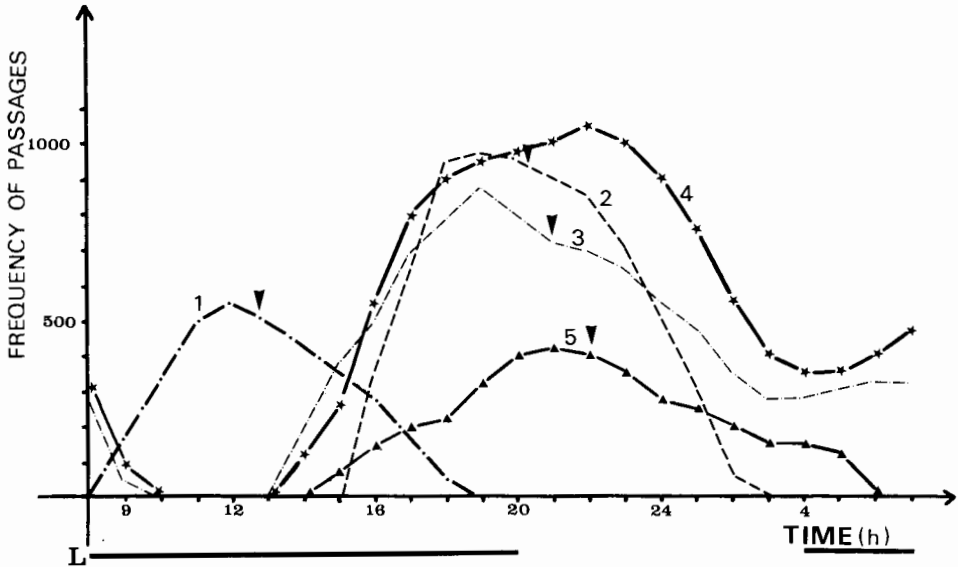

FIG. 2. — Activity rhythm (automatic recording) of four ant species in the Mediterranean region (near Apt, 500 m high) in July 1984 (solar time). The arrows indicate the activity peak. Nest entrances of *C. cursor* (1), *Camponotus aethiops* (2), *Messor structor* (3). Feeders for *M. structor* (4) and *Pheidole pallidula* (5). *M. structor* shows very low foraging activity (curve 4 not shown).

TABLE 1. — *Activity peak and density of four ant species near Apt (altitude = 500 m). All peaks are significant by the Rayleigh test. Density data were obtained in July 1984 on the basis of 12 measures at times when all species are active (7-10 am, 2-6 pm). The densities are all different between species, and between places (t-test).*

	Activity peak (SD)		Density N ants/m² (SD)	
Species	May 1985	July 1984	Shaded places	Sunny places
Cataglyphis cursor	15 hrs. 23	12 hrs. 48	1.58	1.14
	(02 hrs. 22)	(02 hrs. 06)	(0.26)	(0.27)
Camponotus aethiops	15 hrs. 06	20 hrs. 12	27.8	20
	(03 hrs. 47)	(02 hrs. 20)	(2.48)	(1.5)
Messor structor	13 hrs. 15	21 hrs. 06	40.25	35.8
	(4 hrs.)	(04 hrs. 10)	(2.56)	(2.3)
Pheidole pallidula	16 hrs. 07	22 hrs. 00	243.2	123.75
	(3 hrs.)	(03 hrs. 06)	(32.3)	(10.8)

It can be seen from figures 2 and 3 that the four studied species show an activity rhythm. Circular statistics (Rayleigh test, described *in* BATSCHELET, 1981)

were used to verify the existence of an activity rhythm. Rhythm seems to be related to season (Table I). *C. cursor* is a strictly diurnal ant, but, in spring its activity peak is later in the afternoon (15 hrs. 23 min. vs 12 hrs. 48 min.). In the summer *C. cursor* is the only active ant species during the hottest hours of the day. The other ants are inactive, their activity peak being later in the evening. In spring all the ants show diurnal activity. Activity rhythms do not seem to be endogenous but temperature dependent.
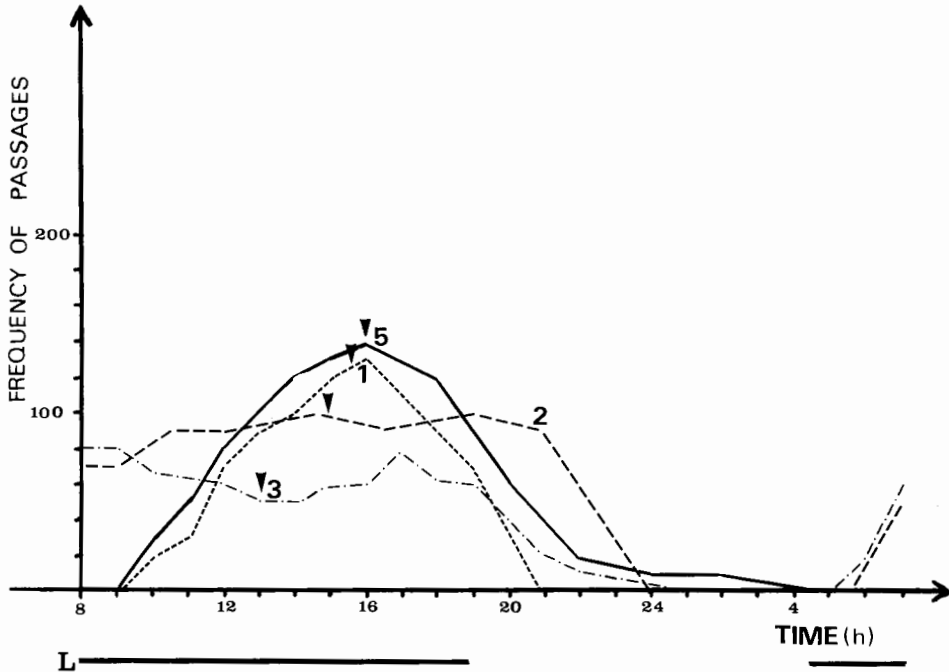

Fig. 3. — Activity rhythm of four ant species in May 1985 (see fig. 2).

NEST DENSITY

C. cursor is widespread in the Mediterranean region. We find small areas with a high nest density, connected by paths (for ex. roads) where dispersed nests are found (CAGNIANT, pers. comm.). The first place studied was an abandoned platform on a camping site near Le Muy (Var). On a surface of 400 m², 25 nests were located representing a theoretical density of 625 nests/ha (see fig. 1 *in* LENOIR *et al.*, 1988, Table II). The second location was near Apt (Vaucluse) in an abandoned lavender cultivation. On the 400 m² studied we found 44 colonies (1,100 nests/ha). It should be noted that a single survey of superficial craters is not sufficient to localize all the nests in a given site. In Le Muy, over 4 days of observation, we located 16 nests (that is only 64% of the total); in the following 6 days, using prey transport experiments, we discovered a further nine nests. These nests were concealed for example in a slope with a single small hole entrance. *C. cursor* typically lives in flat areas, but this preference is not complete.

R values in the studied population are close to 1; nest distribution is therefore random. An analysis of variance on the mean distances between the two populations gave $F=3$ ($P < .01$). This indicates a difference between Apt and Le Muy. Observations suggested that the grassland in Apt was very rich in various insects, with a typical Provencal climate; the platform in Le Muy was much more arid. We hypothesize that differences between the two populations could be explained by differences in the densities of available food.

TABLE II. − *Statistics obtained by using the nearest neighbour distance measure for C.* cursor *nests in two populations. N = Number of distance measures. rA = mean distance to nearest neighbour (min-max). rE = expected mean distance. R = degree to which the observed distribution departs from random expectation. C = standard deviation of the normal curve. NS = non significant.* ([1]) *Assumed on a mean of 600 workers per colony and a fresh weight of 7.2 mg per ant (after Lenoir et al., 1988).*

Site	Surface (m²)	Number Nests N	Biomass ([1]) (kg/ha)	rA	rE	R	C
1 Le Muy	400	25	2.7	2.4 (0.5-5.7)	2	1.2	0.209 NS
2 Apt	400	44	4.75	1.38 (0.55-2.5)	1.5	0.92	0.119 NS

EXPLOITATION OF THE HABITAT

Preliminary observations: diet and observation of individual foragers

When a worker finds a prey, she retrieves it with her mandibles and returns directly to the nest in a straight line. When the ant arrives at the nest entrance, she generally enters the nest immediately, but occasionally deposits the prey 0.5-1 cm from the hole, enters the nest for a few seconds and comes back very quickly to seize the prey and definitively enters the nest. Foragers are always solitary and never cooperate: their density on the ground is very low (about $1/m^2$ for all the nests) in both sunny and shaded places (table I). For the three other species studied, there are 20 to 40 foragers (*Camponotus aethiops, Messor structor*) or more (up to 250 for *Pheidole pallidula*). *Cataglyphis* workers can easily individually retrieve a prey weighing up to 50 mg (the fresh weight of a transporter worker is 15 mg maximum). Prey weighing more than 80-90 mg are abandoned (RETANA, pers. comm.). Individual workers were followed during their foraging trips. They show a tendency to exploit a limited area. When they leave the nest they go in a more less constant direction in successive trips. This is well known in *C. bicolor* (HARKNESS & WEHNER, 1977; WEHNER *et al.*, 1983; SCHMID-HEMPEL, 1987). In this species forager life-expectancy is very short, estimated by SCHMID-HEMPEL & SCHMID-HEMPEL (1984) to be approximately 16 days. A similar phenomenon probably exists in *C. cursor*.

Foraging Experiment 1

In a first experiment we tried to determine the area explored by foragers. Foragers of four neighbouring colonies were marked for several days with different colors. During a one day activity period the ants were counted every 15 minutes on each 1 m × 1 m quadrat. The surface of the total area explored was measured
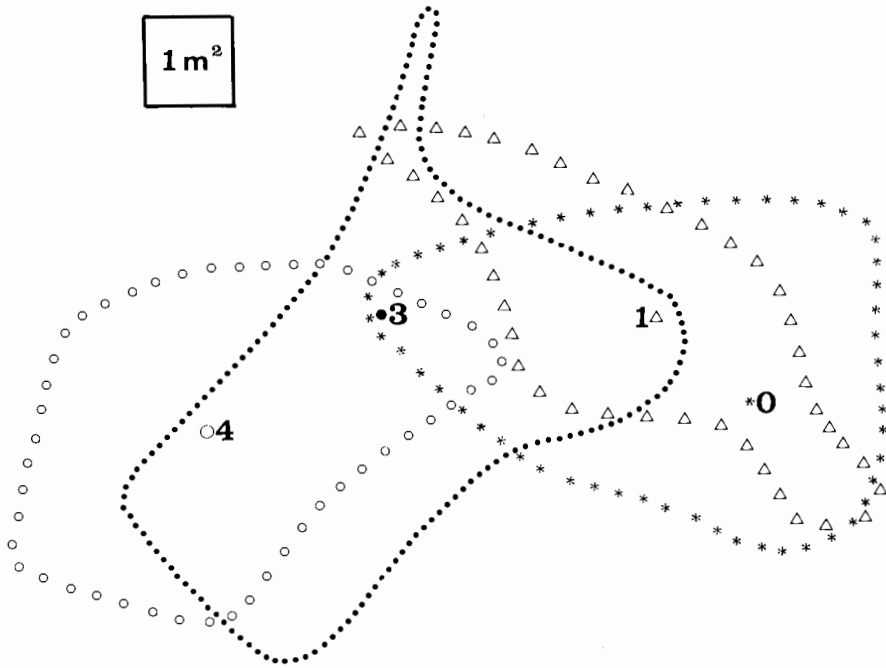
FIG. 4. − Foraging area in four colonies of *C. cursor.*

(fig. 4) and the theoretical mean surface calculated (considered as a circle, the radius being the mean distance of foraging trips observed). Total surface varied from 12 to 18 m^2 and the theoretical mean surface from 4 to 7 m^2. The maximum distance of a foraging trip was 4.4 m. It should be noted that during the observation day the weather was cloudy; as will be seen later we have reason to think that the normal foraging range is greater. Figure 5 shows also that there is considerable overlap between societies: workers forage on foraging ranges of other colonies without incidents, and may even travel near the entrance of an alien nest. However, overall density decreases near alien nests. Overlapping between total surface varies from 0 (colonies 0 and 4) to 50%.

Foraging Experiment 2 (fig. 5 and table III)

A small dead prey (*Camponotus cruentatus* worker, or *Lasius niger* queen) was deposited in the center of a quare and the behaviour of the forager who found it was recorded as (1) time necessary for the discovery, (2) time necessary to return to the nest, (3) locality of the nest and (4) the distance of the trip, together with the speed with which the ants travelled. Each square was tested three times, although not consecutively, so as to avoid a memory phenomenon, as observed in individual foraging ants (DENEUBOURG *et al.*, 1987). For each nest the total foraging area and the theoretical area for successful foragers was determined. The theoretical area was calculated by the method of JORGENSEN & PORTER (1982). The center of the theoretical foraging range is the geometric center of the foraging points, and
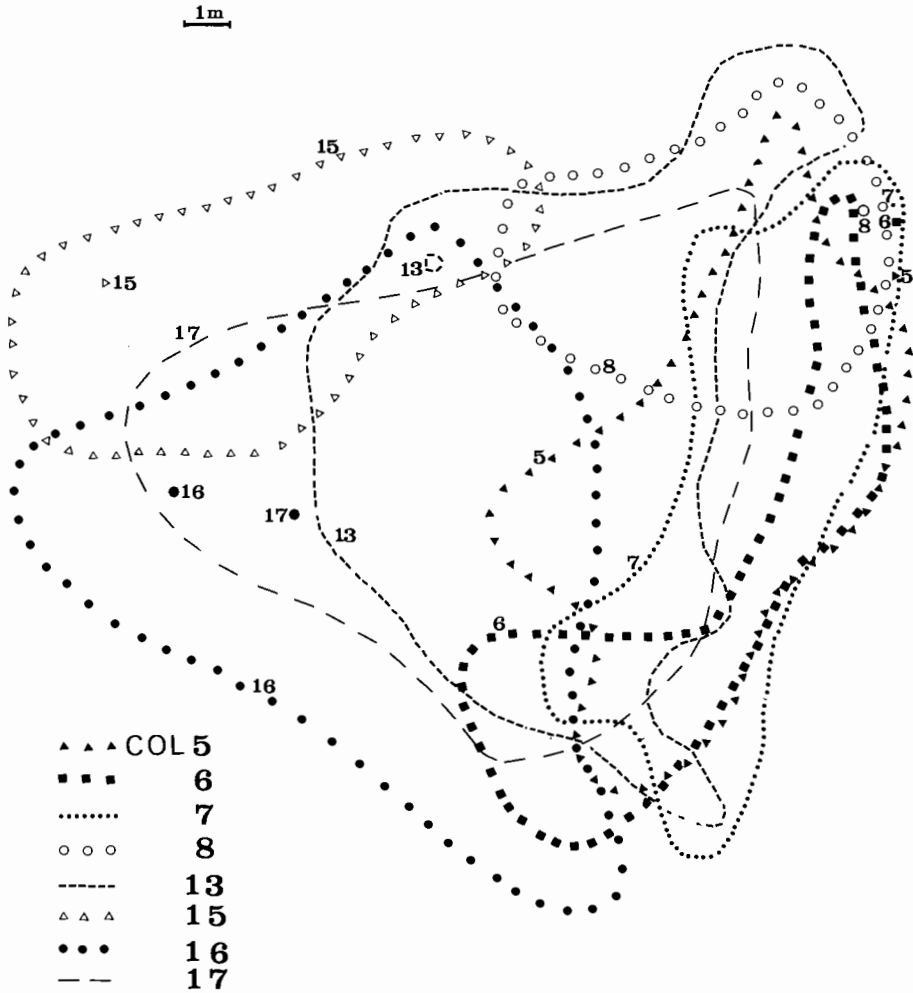
FIG. 5. — Foraging area of eight colonies of *C. cursor*.

TABLE III. — *Characteristics of foraging trips and foraging areas for 14 colonies (theoretical foraging areas calculated for more than 8% retrieved items, i. e. 6 colonies).*

	Foraging trips			% of items retrieved ($n = 264$)	Total explored foraging area (m^2)	Theoretical foraging area (m^2)
	Mean length (m)	Mean duration (min.)	Mean speed (m/min.)			
Mean	5.77	5.78	1.56	6.33	32.93	63.52
Sd	2.72	2.64	0.72	6.22	28.65	38.19
Min-max	0.5-16.5	0.1-45	0.66-6.2	0.7-17.8	4-116	19.6-129.4

the radius is the average distance from the geometric center to the foraging points. A substantial overlap of foraging ranges was observed (maximum 38.7%, mean = 23.3% for $n = 19$). When nests are very close to each other, their foraging area is smaller; this may indicate competition for food or a greater abundance.

95% of the prey were retrieved by *C. cursor* workers, the other 5% were captured by a spider or a bug, or abandoned after difficulties with transport through the vegetation. The maximum distance of foraging trips was 16.5 m, which was similar to other observations made near Port-Leucate. The speed of ants was 0.06 m/min. (3.6 m/hr.) to 6.2 m/min. (372 m/hr.). These data agree with those reported by BERNARD (1984): 5.65 m/min. without prey.

Foraging Experiment 3

Ten small transportable prey items were deposited between two adjacent nests (A and B). The preys were taken to the adjacent nests in variable proportion (table IV A): from 7.5% to 90% when the nearest nest was less than 1 m. There is perhaps a relation between colony size and nest activity, as indicated by SCHMID-HEMPEL (1987).

Foraging Experiment 4

A large unshiftable prey (grasshopper more than 5 cm long) was deposited between two adjacent nests (A and B). The mean number of ants observed licking haemolymph or trying to cut pieces of the prey is essentially constant during the
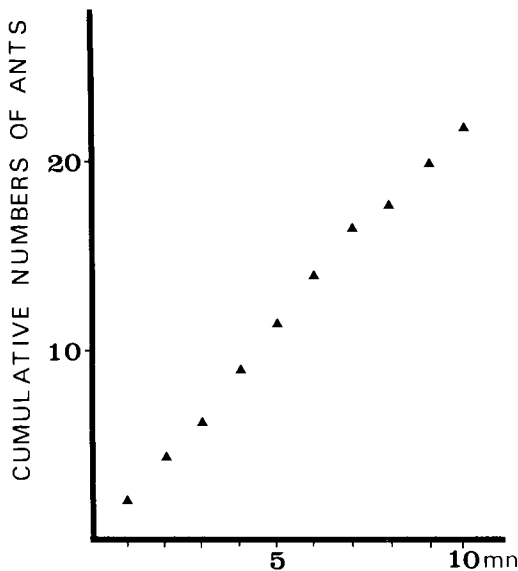

FIG. 6.   Cumulative number of ants of colony A eating a grasshoper. $y = 0.133 + 2.23 x$
($r = 0.998$, $t = 40.92$, 8 df.) Each point is the mean of six measures.

first 10 min. (mean 2.4) (fig. 6). The cumulative curve is linear. This means that there is no recruitment for large unshiftable prey in *C. cursor*. After 10 min., *Pheidole pallidula* workers generally arrive at the prey and chase away the *C. cursor*

workers. *Pheidole* have an efficient mass recruitment system and exploit unshiftable prey. In a few hours the grasshopper was completely eaten by *Pheidole* as observed by DELALANDE (1986).

During these experiments the ants were generally peaceful, but aggressive reactions were observed from time to time, indicating discrimination between societies.

Foraging Experiment 5

The food source (either 10 small transportable preys or a honey drop) was placed next to the nest entrance (less than 5 cm away). There is considerable

TABLE IV. − *Prey retrieval of small items (dead ants) by different nests of* C. cursor *(in % of available prey). The experiments are based on seven different nests. A:* 10 *prey deposited in between nests A and B (*Exp*. 3). B:* 10 *prey deposited at the entrance of nest A (*Exp*. 5).*

		Nest			Number
		A	B	Other	replicates
A-Exp 3					
	40 cm	5%	70%	25%	4
(distance between nests)	60 cm	28.75	61.2	10	8
	110 cm	15.5	36.7	47.8	9
B-Exp 5		70%		30%	11
		94.5		5.5	9
		8.3		91.7	6
		72.5		27.5	40
		57.5		42.5	40
		87.5		12.5	40
		37.5		62.5	50

variation between nests in interest in the prey (Table IV B). More than 50% of prey are generally transported into the nest, but for one nest this value is only 37.5% and only 8.3% for another nest. This is due to the low level of activity shown by these nests, so offered prey were available for foragers of neighbouring nests. For the most active nest, the maximum level of prey retrieval is 94.5%. Thus there is always some poaching between nests, which can occur only a few cm from the nest entrance. Aggressive behaviour appears in this situation but was not observed more frequently than in experiment 3. On the drop of honey we observed also intercolonial competition: a worker arriving on the food may drive out another even if there is available space.

The cumulative number of ants on a honey drop is a linear function of time (fig. 7), both for the focal colony and for the first neighour colony. This clearly indicates the absence of recruitment. This means that when a food source is available near the entrance it is exploited preferentially by the concerned colony (mean 60%, i. e. 3.5 workers) but 22.5% (1.2 workers) for the neighbours and the nest (17.5%, 0.9 workers) for other colonies. This figure is not insignificant. Individual workers were followed when feeding on honey: the mean feeding time was 3.34 min. ($n = 72$). Ants frequently show a staggering gait for some seconds after leaving the honey; they then return directly to their nest.
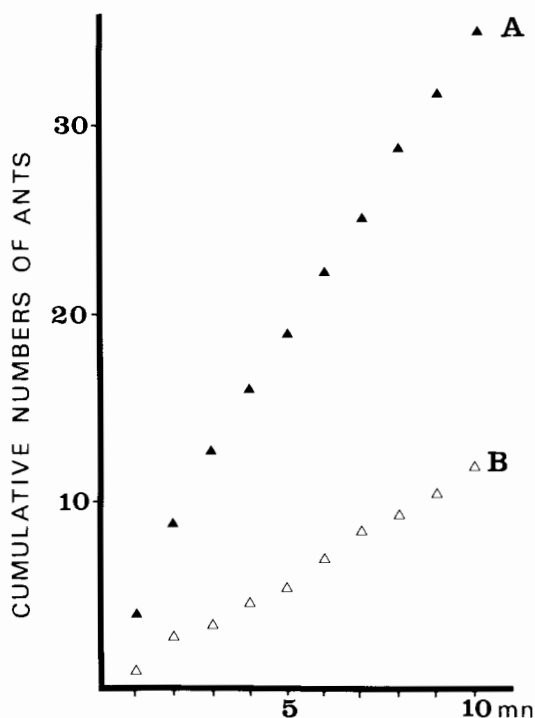
FIG. 7. − Cumulative number of ants feeding on a drop of honey placed near the entrance of a colony A: A, ants of colony A; B, ants of the first neighbour colony B. Curve A: $y = 1.907 + 3.364 x (r = 0.998,$ $t = 52.96,$ $8 df.,$ $P < .001).$ Curve   B: $y = 0.213 + 1.161 x (r = 0.998,$ $t = 50.007,$ $8 df.,$ $P < .001).$ Each point is the mean of 15 measures, 4 colonies tested.

DISCUSSION

Diel variation of activity

All *Cataglyphis* species are strictly diurnal and thermophilous. Their greatest activity takes place when the temperature is highest. CERDA *et al.* (1989) found a strong correlation between activity level and ground surface temperature. When the temperature is between 15 and 30°C, activity is very low, it then increases to a maximum between 43 and 53°C. At 55°C activity drops, and on the hottest days in 4 years observation, CERDA observed a bimodal activity curve. In the south of France the temperature was never so high, and the activity curve was always unimodal. DELYE (1967) found similar data, with a lethal temperature of 55°C for *C. cursor*. In the laboratory NOWBAHARI (1988) observed bimodal activity with a peak during morning hours, unless temperature in the foraging area was 30-35°C.

In the Namibia desert *Ocymyrmex barbiger* is also a diurnal scavenger ant foraging showing a greater activity in the morning. During the hottest days, when temperature can be 68°C there is a bimodal activity with a cessation of activity at midday. The optimal foraging temperature of this species seems to be between 52 and 56.5°C (MARSH, 1985).

In *C. bicolor* the majority of workers leave the nest for foraging during the morning hours (SCHMID-HEMPEL, 1987).

The other three ant species studied in Provence have variable rhythms, switching from diurnal to nocturnal activity with increasing temperatures (from spring to summer), as observed in semi-arid ant communities of Australia (BRIESE and MACAULEY, 1980).

Nest distribution and density

We found a very high density for *C. cursor* colonies: theoretically 600 to 1,000 nests per hectare (projected from subsampling), with a distance between nests varying from 0.5 to 5.7 m. The studied places were chosen for their richness in *Cataglyphis*; in many other more arid habitats, density is no more than 1 nest per 100 m^2 (100/ha). Density is likely related to the level of prey found in the habitat. In a study on ants at the Col de la Bataille (Pyrénées Orientales) on the edge of a vineyard, CAGNIANT (1976 a) found 19 colonies of *C. cursor* (380/ha) which represented 38% of all the ant species. BERNARD (1983) found that in the Mediterranean region *C. cursor* represents 4.2% of the ant nests, with 2 to 4 nests per 100 m^2 (200-400/ha). This author reported a location in the Vaucluse with 25 nests per 100 m^2 (2,500/ha); which was the richest level found in 950 samples from various locations. It should be noted that *C. cursor* is completely absent in forest and in all places where vegetation is dense (for example in Apt it is very rare in the middle of abandoned lavender cultures).

Nearest neighbour distance index indicates that nests of *C. cursor* are randomly distributed. This result is not frequent in social insects: nests are generally regularly distributed. LEVINGS and TRANIELLO (1981) found 67 species (out of 80 from various ant genera) overdistributed and suggested that no colony can establish itself or forage within the foraging area of another colony. *Myrmicaria eumenoides* from the west African savanna also has a clumped distribution, although the distribution is random within a given clump (LEVIEUX, 1983). *Nothomyrmecia macrops* (WARD & TAYLOR, in LEVINGS & TRANIELLO, *op. cit.*) is another randomly-distributed species, which also does not defend territories. *C. bicolor* seems to be overdispersed (SCHMID-HEMPEL, 1987) with a low density of 11.2/ha.

The foraging range of a nest of *C. bicolor* roughly consists of a circular area of 6,000 m^2; only a few trips extend beyond the average nearest-neighbour distance. The smaller competitor *C. albicans* is more abundant with 105.3 nests/ha (*op. cit.*). *C. fortis*, an endemic of salt plains in North-Africa lives in places where other ants cannot survive. Food is very rare and foraging trips frequently cover 150 m (WEHNER, 1983). The smaller species *C. albicans* living in other places have foraging trips which do not exceed 10 m (*ibid*).

The absence of territorial behaviour

The concept of territoriality has two aspects: the restriction of behaviour to a limited area and defense of this area (HÖLLDOBLER, 1979; HÖLLDOBLER & LUMSDEN, 1980). It appears that *C. cursor* is not a territorial species: the nest entrance is not guarded and alien foragers may enter. SHALMON (1982) found a similar result for five Israeli species of *Cataglyphis*, but he suggests that a very small area around the nest entrance is protected: guarding is efficient up to 26 cm. A similar situation is observed in *Nothomyrmecia macrops* where workers of various colonies can

forage peacefully on the same tree. The nest entrance is recognized by odour, and intruders are sometimes attacked, sometimes not (HÖLLDOBLER & TAYLOR, 1983).

Although it is generally considered that many social insects show aggressive behaviour toward heterocolonial individuals, documentation on territorial behaviour has been established in only a few species. It has been observed in termites by LEVINGS & ADAMS (1984) for two species of *Nasutitermes*. The defence of foraging grounds characterizes species with a complex mass-recruitment mechanism and high level of intra and interspecific aggression which can be considered truly territorial. Most dominant tropical canopy ants are in this category and show a mosaic distribution (LEVINGS & TRANIELLO, 1981). Territoriality is usual in *Pogonomyrmex* (HÖLLDOBLER, 1976). Generally, ant species that form relatively small societies do not establish foraging territories (HÖLLDOBLER & LUMSDEN, 1980), but exceptions are not rare as signaled by LACHAUD *et al.* (1984) for *Neoponera apicalis*.

Individual foraging

C. cursor, like other species of *Cataglyphis*, is an individual forager ("diffuse foragers" of OSTER & WILSON, 1978). Recruitment was never observed. SCHMID-HEMPEL (1987) came to the same conclusions for *C. bicolor*. This paper confirms that there is no stimulation of nestmates to start a foraging trip. This can be related to the fact that the various species of *Cataglyphis* show weak response to the alarm pheromone of DUFOUR gland (with the possible exception of *C. livida*; HEFETZ & ORION, 1982).

Individual foraging exists in some Dacetini, many Ponerinae, and some of the non-leaf-cutting Attini (BROWN & WILSON, 1959; WILSON, 1971; OSTER & WILSON, 1978; LEVINGS & TRANIELLO, 1981). In recent studies it has been found that in *Nothomyrmecia macrops* from Australia foragers do not recruit or cooperate; they find the nest entrance using visual cues (HÖLLDOBLER & TAYLOR, 1983). *Ocymyrmex velox*, living in the Namibia desert of South Africa, also shows individual foraging with sector fidelity (WEHNER, 1987) but there is a possibility of recruitment (MARSCH, 1985).

In Mexico LACHAUD *et al.* (1984) and FRESNEAU (1985) found three species of ponerine ants using an individual strategy. In *Neoponera apicalis* all foragers show a marked fidelity to their individual foraging territories and the routes to them. The same foraging pattern is observed in *Ectatomma ruidum* except for the route precision. In *Neoponera villosa*, only a fraction of the foragers show territorial specialization. All three species lack recruitment except for nest-moving by tandem-running. In *E. ruidum* temporary group trails can sometimes be observed; this species is also able to adopt an archaic mass recruitment by activation of foragers in the sector (LACHAUD, 1985).

We should also note the existence of individual foragers in temperate climates: *Formica rufibarbis* (DELALANDE & LENOIR, 1984; DELALANDE, 1986) and *F. cunicularia* (ROISIN, 1982; DEFFERNEZ, 1989) are two thermophilous ants which do not use trails.

CONCLUSION

Individual foraging is not related to the phylogenetic relationship. Rather, it appears to be an adaptation to a particular diet. Corpses are unpredictable in both locality and quantity (CARROLL & JANZEN, 1973). Individual searching without recruitment and without defended territory is a successful strategy. The method is efficient if food items can be handled by a single individual. These ants do not seem adapted to feed on large items which are exploited by other species using mass recruitment (e. g. *Pheidole pallidula* in the Mediterranean region). Spatial fidelity in individual foraging species can be studied by mathematical models, paying attention to the number of animals able to forage, the diversity and the predictability of prey. Results suggest that learning by successive reinforcements regulates the division of labour and spatial fidelity (DENEUBOURG *et al.*, 1987).

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