

Research article

Collective exploration and area marking in the ant *Lasius niger*

C. Devigne and C. Detrain

Laboratoire de Biologie Animale et Cellulaire, CP 160/12, Université Libre de Bruxelles, Avenue F.D. Roosevelt 50, B-1050 Bruxelles, Belgium,
e-mail: cdevigne@ulb.ac.be, cdetrain@ulb.ac.be

Received 21 December 2001; revised 18 June 2002; accepted 25 June 2002.

Summary. The aphid tending ant species, *Lasius niger* collectively explore new areas. Scouts are mobilised within the first five minutes of exploration with activity thereafter decreasing and stabilising after 40 minutes. Collective path choices of colonies underline the existence of chemical recruitment and area marking during exploration.

To identify the territorial or home-range role of exploratory marking, we examined its influence on agonistic behaviour during intraspecific encounters. Ten nestmates and ten alien conspecifics were confronted: (i) on a paper marked by their own colony, (ii) on a paper marked by the alien colony or (iii) on a paper not chemically marked by ants. Residents and intruders showed a weak level of aggression and behaved similarly whatever the type of area marking. As no colony-specificity was observed in the odds of eliciting aggression, exploratory area marking in *Lasius niger* seems to be rather a home-range than a true territorial marking.

We discuss the role of collective exploration, home-range marking and intraspecific interactions in the structuring and use of foraging space by neighbour *Lasius niger* colonies.

Key words: *Lasius niger*; collective exploration, home-range marking, intraspecific interactions, ants.

Introduction

Exploration by scouts allows ant societies to achieve vital activities such as the discovery of food resources or the detection of competitors. Exploration is also a means for ants to improve and update their general knowledge of the nest surroundings. Exploration relies at the individual level on learning processes (e.g. memorisation of visual cues) but also at the collective level, on chemical area marking by scouts. Indeed, scouts can lay actively or passively chemical compounds that define the colony territory or home range (Cammaerts et al., 1977; Hölldobler and Wilson, 1977b;

Jaffe and Puche, 1984; Jaffe and Sanchez, 1984). These chemical marks determine, at least partially, where individuals settle, how long they stay and how they react during agonistic encounters or competition for resources. Such changes of behaviour can give an edge to foraging ants when competition for resources occurs (Hölldobler, 1976; Hölldobler and Wilson, 1977a; Mercier et al., 1997).

Strictly speaking, territorial marks are colony-specific compounds used to identify the terrain as belonging to the colony and as being subject to defence against intra- and interspecific intruders (Hölldobler and Wilson, 1990). Territorial defence does not necessarily mean strong aggressive behaviour and killing as it can simply imply displacing another from an area. Less than 17% of ant species reviewed by Levings and Traniello (1981) actively defend the entire space they use, territories being most often limited to the nest and/or the feeding places (Brown and Orians, 1970). Beside chemical marking, encounters between neighbouring colonies can also determine the boundaries of their respective foraging ranges as seen in the harvester *Pogonomyrmex* ants (Gordon, 1992, 1995; Gordon and Kulig, 1996). Among the ecological consequences of territoriality are spatial patterns of nest distribution (Caroll and Janzen, 1973; Hölldobler, 1976; Bernstein and Gobbel, 1979; Levings and Franks, 1982; Traniello and Levings, 1986; Rytty and Case, 1986; Gordon and Kulig, 1996) and/or patterns of foraging trails that direct ants of adjacent nests into diverging directions (Hölldobler, 1976; Hölldobler and Lumsden, 1980; Hölldobler and Möglich, 1980; Traniello, 1989).

In contrast to territorial marking, home-range marking labels areas that the colony knows to be hospitable and available for foraging but does not defend against intra and interspecific intruders (Hölldobler and Wilson, 1990). Indeed, several ant species visually and/or chemically perceive that they are on their home-range without exhibiting aggressive behaviour towards intruders (e.g. *Pogonomyrmex* (Hölldobler, 1976); *Myrmica rubra* (Cammaerts et al., 1977); *Solenopsis geminata* (Jaffe and Puche, 1984), *Polyrhachis laboriosa* (Mercier et al., 1997)). The home-range perception

influences the individual behaviour of ants by improving their orientation (Fourcassié, 1986; Cammaerts and Cammaerts, 1987; Fourcassié and Beugnon, 1988; Wehner, 1992), by increasing their moving speed (Cammaerts and Cammaerts, 1996) or by enhancing the intensity of recruitment (Hölldobler, 1976). Home-range perception is hence one of the key factors that shape the global use of space by a colony.

Here we will study the exploration behaviour of the aphid-tending ant *Lasius niger* when confronted with new foraging areas. Since *Lasius niger* is assumed to lay chemical marks during exploration (Yamaoka and Akino, 1994), we will investigate whether such marking actually occurs and whether it influences collective patterns of exploration. We will examine the colony specificity of exploratory marking and its influence on agonistic behaviour during intraspecific encounters. This will lead us to identify the territorial or home-range role of exploratory marking in *Lasius niger*. Ultimately, we will discuss the impact of area marking on between-colony interactions within ant communities.

Material and methods

Collection and rearing of colonies

Ten colonies of *Lasius niger* with about 500–1000 individuals were collected in Belgium (Brussels) and in France (Proisy). They were reared in the laboratory within plaster nests (20×20 cm) divided into three connected lodges. Nests were placed in plastic trays (48×34×7.5 cm) the sides of which had been coated with Fluon to prevent ants escaping. The nest plaster was moistened twice a week. Room temperature was kept at $23 \pm 2^\circ\text{C}$. Colonies had a permanent access to a sugar solution (1M) and water, and were fed with dead cockroaches (*Periplaneta americana*) once a week.

Experimental procedure

Collective exploration of new areas

Nine colonies of *Lasius niger* were starved for three days, and then allowed to reach two separate foraging areas by a Y-shaped cardboard bridge. The two branches of the bridge were 30 cm length (1 cm wide) and were separated by a 30° angle. In order to prevent orientation bias due to the use of visual cues, we surrounded the whole experimental set-up with a 50cm high opaque enclosure.

The Y-shaped bridge was chosen because it allowed us to evidence, with a higher accuracy, amplifying processes such as recruitment depending on the perception of chemical marks by ants. The existence of chemical marks laid by ants and their influence on collective decisions during exploration were assessed by observing the distribution of workers over each branch of the bridge. For thirteen experiments, the number of individual ants outgoing were counted at the bifurcation point of the bridge during fifteen minutes after forty five minutes of exploration of the new areas. A branch was considered as selected when the binomial test concluded that a significantly higher number of workers followed that branch (0.05 level of significance). Besides, in order to draw the global dynamics of the exploration, we measured in seven experiments the flows of individual ants outgoing during the whole one hour exploration.

Role of area marking

Eight colonies of *Lasius niger* had access for six days, via a cardboard bridge (30 cm length), to a foraging platform (10×10 cm) covered with

a piece of filter paper (9 cm diameter) that scouts could chemically mark during their exploration.

After six days of acclimatisation, 10 ants were confronted with 10 conspecifics from another colony within a Petri dish of which the surface was covered with the filter paper, putatively marked chemically by the ants. We allowed ants of each subgroup to calm down by keeping them separated for five minutes in two bottomless cylinders (2 cm diameter, 4 cm high) placed on the surface of the Petri dish. The cylinders were then removed and the behaviour of ants were video-recorded for one minute. Preliminary experiments showed that longer lasting observations of five minutes led to similar conclusions than those lasting one minute.

Ten *Lasius niger* ants were confronted with ten alien conspecifics in one of these three conditions: (i) on paper marked by their own colony, (ii) on paper marked by the alien colony or (iii) on paper not chemically marked by ants.

One experimental series of these three conditions was carried out during the same day, with conditions being tested in random order. Each colony was used only for one experimental series and groups of tested ants were changed between successive experiments. Experimental series were replicated four times.

For each ant, we measured the absolute distance covered during one minute, the number of encounters and the number of agonistic behaviour. We considered an ant as showing agonistic behaviour when it bit or tried to bite another ant. We quantified vigorous back-and-forth jerkings of the body which are characteristic behaviour of workers involved in tournaments between neighbour conspecific colonies (Czechowski, 1984). We also measured the duration of encounters between either nestmates or foreigners in additional experiments ($n = 9$) of paired confrontations over unmarked and marked areas.

To limit potential bias due to the aggregation of ants close to the Petri dish walls, these behaviour were quantified in a smaller circle (7 cm diameter) centred in the middle of the Petri dish. The number of ants present in this smaller circle was quantified every ten seconds during the whole experiment.

The speed of ants in the different experimental conditions were compared using ANOVA tests. Fisher's exact test was used to compare the observed probability for an ant to encounter an intruder with that expected from random. The proportion of aggressive encounters and jerking behaviour between experimental conditions were compared using χ^2 tests and if a difference was observed, a Tukey-type multiple comparison was used to point out significant differences between groups.

Results

Collective exploration of new areas

As soon as a nest was connected to a new foraging area, a flow of exploring ants was observed over the bridge. The peak flow of ants was reached in the first five minutes of exploration at approximately 100 ants/5 min (Fig. 1). During the one hour of exploration, the flow of ants progressively and significantly decreased, stabilising after 50 min at around 60 individuals/5 minutes (Fig. 1, Paired ANOVA test; $p < 0.001$).

When exploring the new area, scouts were not seen actively laying trails by contacting the tip of their gaster with the substrate like when they recruit to food sources (Beckers et al., 1992). Although no active trail-laying behaviour was observed during exploration, indirect evidence suggested the existence of chemical recruitment, through the occurrence of bifurcation of flow of ants towards one of the two branches in 53.8% of experiments (Table 1). However, the selection of a

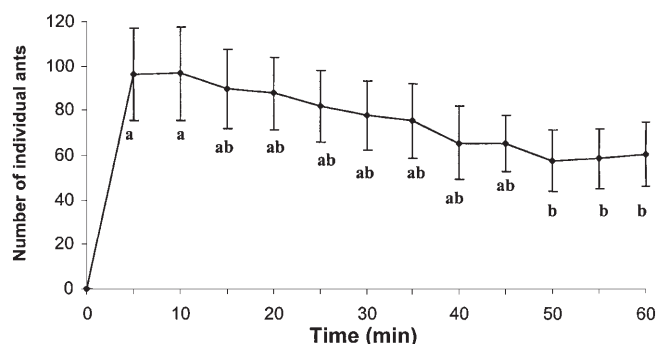


Figure 1. Number of individual ants walking over the bridge towards new foraging areas with time. Numbers of ants walking over the two branches of the bridge were summed per five minute intervals and were averaged (\pm SE) over the 7 experiments. Means sharing the same letter were not significantly different (Tukey multiple comparison test)

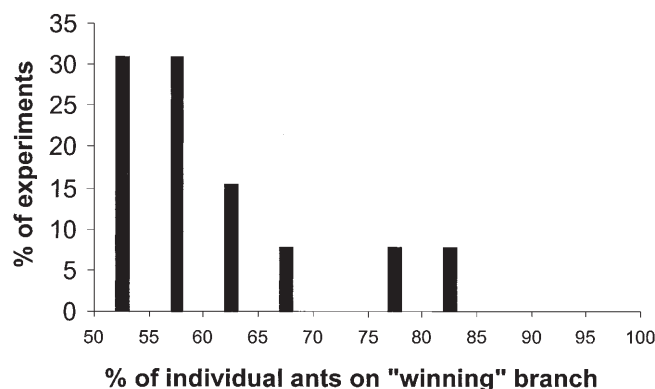


Figure 2. Distribution of experiments as a function of path selection expressed as the percentage of all of the ants on the "winning" branch (N = 13)

Table 1. Ants' flows during exploration of new areas. Flows of ants were measured during the last 15 minutes of one hour exploration and 15 minutes after 20 hours of exploration. The percentages of experiments in which there was a choice of one branch are given. A branch was considered as selected when the binomial test was significant ($p < 0.05$)

	1 hour of exploration	20 hours of exploration
Number of ants/ 15 min	107.5 \pm 110.4 (13)	37.13 \pm 37.5 (15)
Mean \pm SD (n)		
% experiments where a branch was selected (n)	53.8 (13)	18.2 (11)

branch was never strong, with the proportion of ants on the "winning" branch exceeding 70% in only 16% of experiments (Fig. 2). No clear-cut exploration trail emerged as ants were scattered over the whole area being sometimes "trapped" close to the area border.

After 20 hours of exploration, the average flow of ants strongly decreased with flows of ants being 3 times lower than during the initial phase of exploration (Table 1). The selection of a path occurred in very few cases (Table 1: 2 cases out of 11 experiments) and was very weak with the winning branch carrying, at most, 66% of the individuals.

Role of area marking

Ants moved at a higher speed over chemically marked areas than over unmarked areas, though a significant difference was found only for areas explored by a foreign colony. Over marked areas, ants moved at similar speed whatever the type of exploratory marking (foreign or mother colony: Table 2).

Chemical marking did not significantly influence the distribution of ants over the setup. Indeed, the percentages of ants present in the observation circle were similar among conditions of area marking during the whole experiment (χ^2 tests; all p values > 0.01 for each 10 s interval observation).

Moreover, whatever the experimental conditions, ants from each confronted subgroup showed similar rates of presence in the observation circle that do not differ from the expected value of 0.5 (Binomial tests, all p values > 0.1 for each 10 s interval observation).

Despite this similar rate of presence of ants, we observed higher (though not statistically significant) percentages of encounters between foreigners when the area was chemically marked (Table 2, χ^2 test, $p > 0.1$). Indeed, when the substrate was marked, ants encountered foreigners more frequently than expected from random (G test with the Yates correction: $p < 0.05$ for both marked conditions). These higher percentages of encounters observed on marked areas could not be explained by differences in the duration of interactions between foreigners: contacts lasted on average 10.6 s (\pm 16.2 (SD) N = 107) and 8.5 s (\pm 10.2 (SD), N = 140) over the unmarked and marked setup respectively (Mann-Whitney's test $U = 6885$, $p > 0.2$). This suggests that exploratory marks somewhat influence the rate of foreign encounters and trigger among ants their interest in assessing the force of alien conspecifics.

Whatever the area marking, ants straightforwardly recognized their nestmates: aggressiveness between nestmates during encounters was nil and nestmate contacts lasted significantly shorter than those with foreigners (1.7 s \pm 1.1 (SD) N = 224 and 9.4 s \pm 13.2 (SD) N = 247 respectively; Mann-Whitney's test $U = 7597$, $p < 0.0001$).

By contrast, ants were aggressive in front of alien workers and showed agonistic behaviour in 28 to 48% of encounters. This agonistic behaviour was related to area marking (Table 2: $\chi^2 = 16.2$, $p < 0.001$). Indeed, whatever the type (mother or foreigner) of marking, the percentages of aggressive behaviour in encounters with foreigners were significantly higher over marked areas than over an unexplored setup (Table 2, Tukey-type multiple comparisons test; $Q = 4.55$, $p < 0.005$ for area marked by mother colony vs. no marking and $Q = 5.22$, $p < 0.001$ for area marked by foreigner colony vs. no marking). Area marking, therefore, somehow enhances the level of aggressiveness among ants without any colony specificity. However, the inter-colonial aggressive-

Table 2. Influence of area marking on the behaviour of intruder or resident ants. Mean (\pm SE) are given for the ants' speed. Means or percentages sharing the same letter in superscript were not statistically different. When letters are not present, no differences occur. NA: Not Applicable for χ^2 test (more than 20 % of expected values lower than five)

	Area marked by mother colony	Area marked by foreigner colony	No marking	Statistics
ants speed (cm/s)	2.99 ^(a, b) (\pm 0.22) N = 77	3.03 ^(a) (\pm 0.16) N = 77	2.4 ^(b) (\pm 0.16) N = 73	ANOVA test P < 0.05
% foreigner encounter	59.75 (N = 241)	62.01 (N = 279)	54.31 (N = 348)	χ^2 test N.S.
% aggression in encounters with a nestmate	0 (N = 97)	0 (N = 106)	0.63 (N = 159)	N.A.
% aggression in encounters with a foreigner	45.14 ^(a) (N = 144)	46.82 ^(a) (N = 173)	28.04 ^(b) (N = 189)	χ^2 test p < 0.001
% jerking behaviour in encounters with a nestmate	4.12 (N = 97)	5.66 (N = 106)	8.18 (N = 159)	χ^2 test N.S.
% jerking behaviour in encounters with a foreigner	19.44 (N = 144)	13.29 (N = 173)	18.87 (N = 189)	χ^2 test N.S.

ness was scarcely fierce, predominantly being attempts to bite or jerking behaviour, with effective bites resulting in the death of an opponent being exceptional (5 out of 506 observed contacts).

Ants can also perform jerking behaviour when facing an encountered ant or when touching other body parts such as the gaster. The percentage of jerking behaviour did not differ according to area marking during encounters with a nestmate (Table 2, $\chi^2 = 0.89$; $p > 0.5$) or with a foreigner (Table 2, $\chi^2 = 2.82$; $p > 0.2$). We also noticed that for each marking condition, the percentage of jerking behaviour was significantly higher during inter-colonial encounters than during intra-colonial ones (Fisher's test; $p < 0.001$, $p > 0.05$ and $p < 0.01$ for area marked by mother colony, by foreigner colony and unmarked area, respectively). Moreover, it seemed that certain ants were more prone to display jerking behaviour than others because all of the observed jerking was performed by only 18.6% of the tested ants (N = 231).

Discussion

Lasius niger is a mass recruiting ant species in which amplifying processes based on trail recruitment play a key role. In such a self-organised society (Camazine et al., 2001), group size and more specifically the number of scouts in the vicinity of discovered food sites rules the dynamics of recruitment and is crucial for the rapid emergence of foraging choices (Beckers et al., 1989; Jaffe and Deneubourg, 1992; Gordon, 1995; Burkhardt, 1998; Mailleux et al., submitted). Increasing group size improves the selection of the most rewarding resources (Nicolis and Deneubourg, 1999) and prevents food appropriation by competitors (Adams, 1990; Yamaguchi, 1995). In this respect, collective exploration is a means for the ant's society to bring to new areas, a patrolling force numerous enough to generate efficient foraging responses. Exploration being a collective rather than an individual

process has been reported in several ant species, that differ in their exploratory patterns ranging from a diffuse collective exploration to a cohesive trail (see e.g. Franks and Fletcher, 1983; Aron et al., 1989; Detrain et al., 1991; Fourcassié and Deneubourg, 1992, 1994). Though *Lasius niger* scouts are scattered over the foraging area, more than half of the experiments lead to the collective choice of an exploratory path. Though never strong, this bifurcation of ant traffic supports the existence of an amplification process based on chemical marking (Pasteels et al., 1987; Deneubourg and Goss, 1989). This exploratory marking might be passively left by walking ants and probably consist of foot print hydrocarbons (Yamaoka and Akino, 1994). The relatively weak selection rate suggests that these exploratory marks have a lower attracting effect than the recruitment trail laid by *Lasius niger* during food exploitation since, in this case, 77.8% of experiments (N = 27, unpubl. data) lead to the selection of a branch. One might assume that the attractiveness level of exploratory marks has been selected through the evolution, arising from a trade-off between aggregating ants to improve colony foraging efficiency through cooperation, and dispersing scouts to increase potential food discoveries through the enlargement of the explored home-range.

The chemical marking of explored areas significantly enhanced the agonistic behaviour of conspecific ants, though it remains at a weak level with workers only exhibiting intimidating behaviour (jerkings, attempts to bite) rather than truly aggressive biting. However, the type of the exploratory marking (e.g. laid by the mother colony or laid by another conspecific one) did not differentially alter the aggressiveness of residents and intruders. Area marking does not seem to give an immediate edge for the residents during competitive interactions with intruders. This lack of colony specificity strongly suggests that exploratory area marking in *Lasius niger* is not a territorial but rather a home-range marking (as defined by Jaffe and Puche, 1984; Hölldobler and Wilson, 1990).

Though *Lasius niger* does not lay colony specific territorial marks, this species actively regulates its relationships with neighbouring colonies. The level of aggression displayed by workers to alien conspecifics depends on the presence of surrounding nestmates (Sakata and Katayama, 2001) and on the location of encounters (Levings and Traniello, 1981), as fierce fights and bites are usually limited to food sites and nest area (Dobrzanska, 1958; Pontin, 1961; Brian et al., 1966; Levings and Traniello, 1981). It also depends on the relative worker force of opponent neighbours, with a larger colony often raiding over a smaller one (e.g. Czechowski, 1984; Sommer and Hölldobler, 1995). Most frequently, these intraspecific encounters are mildly aggressive and devoid of fights. Between-colonies contests can also involve tournaments with body jerkings (Czechowski, 1984), allowing ants to intimidate and/or estimate their relative force without mortality risks (as also found in *Myrmecocystus mimicus*: Hölldobler, 1979 and in *Polyrhachis laboriosa*: Mercier et al., 1997). Direct interactions between *Lasius niger* individuals rather than territorial marking thus rule intraspecific competition between neighbour colonies. Similarly in *Pogonomyrmex barbatus*, interactions between neighbours are required to determine and maintain the boundaries of their respective foraging ranges (Gordon, 1992, 1995; Gordon and Kulig, 1996). Moreover, in *Lasius fuliginosus* (Gordon et al., 1993), the rate of encounters with non-nestmates provide a measure of the extent of danger during conflicts between neighbouring colonies.

The lack of territorial marking facilitates the sharing of explored areas between neighbouring colonies of *Lasius niger* that would enlarge their potential foraging space (Hölldobler and Lumsden, 1980; Holway et al., 1998). This could be very helpful for growing foundations or mature colonies during periods of reduced food availability as a means for increasing the chance to discover resource. *Lasius niger* species seem to rely on a "shared information" strategy in which the web of exploratory marks provides to both nestmates and alien conspecifics a spatio-temporal assessment of environmental resources. As for interaction rates (Brown and Gordon, 2000; see also in lizards, Stamps, 1994), conspecific cueing through area marking could influence the choice of a foraging space or of a nest site (Depickere, 1999). Ants may prefer areas previously occupied and marked by alien conspecifics than unmarked terrain. Testing the impact of area marking on foraging of both residents and intruders should be the next step to validate this "shared information" strategy.

Acknowledgments

We warmly thank J.C. de Biseau and D. Fournier for critical discussion and Dr. B. Hoffmann for revising the English manuscript. This study was supported by the Belgian Fund for Joint Basic Research (grant n° 2.4510.01). The Van Buuren Foundation financially supported C. Devigne. C. Detrain is research associate from the Belgian National Fund for Scientific Research.

References

- Adams, E.S., 1990. Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries in colony size. *Anim. Behav.* 39: 321–328.
- Aron, S., J.M. Pasteels and J.L. Deneubourg, 1989. Trail-laying behaviour during exploratory recruitment in the Argentine ant, *Iridomyrmex humilis* (Mayr). *Biol. Behav.* 14: 207–217.
- Beckers, R., S. Goss, J.L. Deneubourg and J.M. Pasteels, 1989. Colony size, communication and ant foraging strategy. *Psyche* 96: 239–256.
- Beckers, R., J.L. Deneubourg and S. Goss, 1992. Trail-laying behaviour during food recruitment in the ant *Lasius niger* (L.). *Insectes soc.* 39: 59–72.
- Bernstein, R.A. and M. Gobbel, 1979. Partitioning of space in communities of ants. *J. Anim. Ecol.* 48: 931–942.
- Brian, M.V., J. Hibble and A.F. Kelly, 1966. The dispersion of ant species in a southern english heath. *J. Anim. Ecol.* 35: 281–290.
- Brown, J.L. and G.H. Orians, 1970. Spacing patterns in mobile animals. *Annu. Rev. Ecol. Syst.* 1: 239–262.
- Brown, M.J.F. and D.M. Gordon, 2000. How resources and encounters affect the distribution of foraging activity in seed-harvesting ant. *Behav. Ecol. Sociobiol.* 47: 195–203.
- Burkhardt, J.F., 1998. Individual flexibility and tempo in the ant, *Pheidole dentata*, the influence of group size. *J. Insect Behav.* 11: 493–505.
- Camazine, S., J.L. Deneubourg, N.R. Franks, J. Sneyd, G. Theraulaz and E. Bonabeau, 2001. *Self-organization in Biological Systems*. Princeton University Press. 535 pp.
- Cammaerts, M.C., E.D. Morgan and R. Tyler, 1977. Territorial marking in the ant *Myrmica rubra* L. (Formicidae). *Biol. Behav.* 2: 263–272.
- Cammaerts, M.C. and R. Cammaerts, 1996. Area marking in the ant *Pheidole pallidula* (Myrmicinae). *Behav. Process.* 37: 21–30.
- Cammaerts, R. and M.C. Cammaerts, 1987. Nest topology, nestmate recognition, territorial marking and homing in the ant *Manica rubida* (Hymenoptera, Formicidae). *Biol. Behav.* 12: 65–81.
- Caroll, C.R. and D.H. Janzen, 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* 4: 231–257.
- Czechowski, W., 1984. Tournaments and raids in *Lasius niger* (L.) (Hymenoptera, Formicidae). *Annls. Zool.* 38: 81–91.
- Deneubourg, J.L. and S. Goss, 1989. Collective patterns and decision making. *Ecol. Ethol. Evol.* 1: 295–311.
- Depickere, S., 1999. Etude de l'influence du marquage territorial sur deux dynamiques: l'agrégation et le recrutement alimentaire chez la fourmi *Lasius niger* (L.). *D.E.A Biologie du Comportement*- Université Paris-Nord: 25 pp.
- Detrain, C., J.L. Deneubourg, S. Goss and Y. Quinet, 1991. Dynamics of collective exploration in the ant *Pheidole pallidula*. *Psyche* 98: 21–31.
- Dobrzanska, J., 1958. Partition of foraging grounds and modes of conveying information among ants. *Acta Biol. Exp.* 18: 55–67.
- Fourcassié, V., 1986. Retour au nid et mécanismes d'orientation chez les ouvrières de la fourmi rousse des bois sur l'aire d'affouragement d'une colonie polycalique. *Actes coll. Insectes soc.* 3: 243–259.
- Fourcassié, V. and G. Beugnon, 1988. How do red wood ants orient when foraging in a three dimensional system? I. Laboratory experiments. *Insectes soc.* 35: 92–105.
- Fourcassié, V. and J.L. Deneubourg, 1992. Collective exploration in the ant *Monomorium pharaonis* L. In: *Biology and Evolution of Social Insects* (Billen, J., Ed.), Leuven University Press, Leuven. pp. 369–373.
- Fourcassié, V. and J.L. Deneubourg, 1994. The dynamics of collective exploration and trail-formation in *Monomorium pharaonis*: experiments and model. *Physiol. Entomol.* 19: 291–300.
- Franks, N.R. and C.R. Fletcher, 1983. Spatial patterns in army ant foraging and migration: *Eciton burchelli* on Barro Colorado island, Panama. *Behav. Ecol. Sociobiol.* 12: 261–270.
- Gordon, D.M., 1992. How colony growth affects forager intrusion between neighboring harvester ant colonies. *Behav. Ecol. Sociobiol.* 31: 417–427.

- Gordon, D.M., E.P. Richard and K. Thorpe, 1993. What is the function of encounter patterns in ant colonies? *Anim. Behav.* 45: 1083–1100.
- Gordon, D.M., 1995. The expandable network of ant exploration. *Anim. Behav.* 50: 995–1007.
- Gordon, D.M. and A.W. Kulig, 1996. Founding, foraging, and fighting: colony size and the spatial distribution of harvester ant nests. *Ecology* 77: 2393–2409.
- Holway, D.A., A.V. Suarez and T.J. Case, 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science* 282: 949–952.
- Hölldobler, B., 1976. Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behav. Ecol. Sociobiol.* 1: 3–44.
- Hölldobler, B. and E.O. Wilson, 1977a. Weaver ants : Social establishment and maintenance of territory. *Science* 195: 900–902.
- Hölldobler, B. and E.O. Wilson, 1977b. Colony-specific territorial pheromone in the African weaver ant *Oecophylla longinoda* (Latreille). *Proc. Nat. Acad. Sci. USA* 74: 2072–2075.
- Hölldobler, B., 1979. Territoriality in ants. *Proc. Am. Phil. Soc.* 123: 211–218.
- Hölldobler, B. and M. Möglich, 1980. The foraging system of *Pheidole militica* (Hymenoptera : Formicidae). *Insectes soc.* 27: 237–264.
- Hölldobler, B. and C.J. Lumsden, 1980. Territorial strategies in ants. *Science* 210: 732–739.
- Hölldobler, B. and E.O. Wilson, 1990. *The Ants*. The Belknap Press of Harvard University Press, Cambridge, Mass. 732 pp.
- Jaffe, K. and H. Puche, 1984. Colony-specific territorial marking with the metapleural gland secretion in the ant *Solenopsis geminata* (Fabr.). *J. Insect Physiol.* 30: 265–270.
- Jaffe, K. and C. Sanchez, 1984. On the nestmate-recognition system and territorial marking behaviour in the ant *Camponotus rufipes*. *Insectes soc.* 31: 302–315.
- Jaffe, K. and J.L. Deneubourg, 1992. On foraging, recruitment systems and optimum number of scouts in eusocial colonies. *Insectes soc.* 39: 201–213.
- Levings, S.C. and J.F.A. Traniello, 1981. Territoriality, nest dispersion, and community structure in ants. *Psyche* 88: 265–319.
- Levings, S.C. and N.R. Franks, 1982. Patterns of nest dispersion in a tropical ground ant community. *Ecology* 63: 338–344.
- Mercier, J.L., A. Lenoir and A. Dejean, 1997. Ritualised versus aggressive behaviour displayed by *Polyrhachis laboriosa* (F. Smith) during intraspecific competition. *Behav. Process.* 41: 39–50.
- Nicolis, S.C. and J.L. Deneubourg, 1999. Emerging patterns and food recruitment in ants: an analytical study. *J. Theor. Biol.* 198: 575–592.
- Pasteels, J.M., J.L. Deneubourg and S. Goss, 1987. Self-organization mechanisms in ant societies (1): trail recruitment to newly discovered food sources. *Experientia* 54: 155–175.
- Pontin, A.J., 1961. Population stabilization and competition between the ants *Lasius flavus* (F.) and *Lasius niger* (L.). *J. Anim. Ecol.* 30: 37–54.
- Ryti, R.T. and T.J. Case, 1986. Overdispersion of ant colonies: a test of hypotheses. *Oecologia* 69: 446–453.
- Sakata, H. and N. Katayama, 2001. Ant defence system: a mechanism organizing individual responses into efficient collective behavior. *Ecol. Res.* 16: 395–403.
- Sommer, K. and B. Hölldobler, 1995. Colony founding by queen association and determinants of reduction in queen number in the ant *Lasius niger*. *Anim. Behav.* 50: 287–294.
- Stamps, J., 1994. Territorial behavior: testing the assumptions. *Adv. Stud. Behav.* 23: 173–231.
- Traniello, J.F.A. and S.C. Levings, 1986. Intra- and intercolony patterns of nest dispersion in the ant *Lasius neoniger*: correlations with territoriality and foraging ecology. *Oecologia* 69: 413–419.
- Traniello, J.F.A., 1989. Chemical trail systems, orientation, and territorial interactions in the ant *Lasius neoniger*. *J. Insect Behav.* 2: 339–353.
- Wehner, R., 1992. Arthropods. In: *Animal Homing* (Papi, F., Ed.), Chapman and Hall Animal Behaviour Series, London, pp. 45–144.
- Yamaguchi, T., 1995. Intraspecific competition through food robbing in the harvester ant, *Messor aciculatus* (Fr. Smith), and its consequences on colony survival. *Insectes soc.* 42: 89–101.
- Yamaoka, R. and T. Akino, 1994. Ecological importance of cuticular hydrocarbons secreted from the tarsus of ants. In: *Les Insectes Sociiaux* (Lenoir, A., G. Arnold and M. Lepage, Eds.) Université Paris-Nord: p.222



To access this journal online:
<http://www.birkhauser.ch>