

C. Detrain · C. Natan · J.-L. Deneubourg

The influence of the physical environment on the self-organised foraging patterns of ants

Received: 24 August 2000 / Accepted in revised form: 16 February 2001 / Published online: 25 April 2001
© Springer-Verlag 2001

Abstract Among social insects such as ants, scouts that modulate their recruiting behaviour, following simple rules based on local information, generate collective patterns of foraging. Here we demonstrate that features of the abiotic environment, specifically the foraging substrate, may also be influential in the emergence of group-level decisions such as the choice of one foraging path. Experimental data and theoretical analyses show that the collective patterns can arise independently of behavioural changes of individual scouts and can result, through self-organising processes, from the physico-chemical properties of the environment that alter the dynamics of information transfer by chemical trails.

A striking feature of insect societies such as those of ants and bees is their ability to co-ordinate behaviours of thousands of individuals and to reach group-level patterns without central or hierarchical control. Collective decisions arise through amplifying phenomena driven by interacting individuals that follow simple behavioural rules based on local information (Deneubourg and Goss 1989; Seeley 1995; Camazine et al. 2001). Such self-organising processes apply to a wide range of group behaviour, including exploration of new areas (Deneubourg et al. 1990, Detrain et al. 1991), nest moving (Visscher and Camazine 1999), nest defence (Millor et al 1999), clustering of brood within the nest (Deneubourg et al. 1991) and foraging (Deneubourg et al. 1989; Franks et al. 1991; Stickland et al. 1993; Detrain and Deneubourg 1997). The most familiar example of decentralised decision-making in ants is the collective choice of one of many food resources that arises through competing

chemical trails which are signals stimulating the ants to exit the nest, and also act as orientation cues channelling foragers to feeding areas. Ant scouts are widely recognised as the primary agents determining the foraging choices of the whole colony, since they decide whether or not to lay a trail and modulate the intensity of their recruiting behaviour according to food characteristics (for a review see e.g. Hölldobler and Wilson 1990; Traniello and Robson 1995; Detrain et al. 1999). In the mass recruiting ant, *Lasius niger*, scouts modify their trail-laying behaviour following functional criteria and local assessment of food, thus enabling the colony to concentrate foragers on top-quality sources (Beckers et al. 1993; Mailleux et al 2000). The biotic environment, including factors such as the distribution and abundance of food resources (see Bernstein 1975; Hölldobler 1976; Rissing and Wheeler 1976; Hahn and Maschwitz 1985), the presence of competitors (see Hölldobler 1976; Acosta et al. 1995) or the existence of predators (see Hunt 1983; Nonacs and Dill 1988), is also known to influence the foraging patterns in ants. For instance, Franks et al. (1991) demonstrate how the distribution and abundance of food acts upon the recruitment dynamics of army ants and thus contributes to the emergence of self-organised raiding patterns. By contrast, the influence of the abiotic environment on the recruitment behaviour of individual ants as well as on collective foraging choices remains widely unknown. We therefore observed the ant *L. niger* to determine (1) whether the surrounding substrate influences the foraging pattern of the colony (selection of a path) and (2) whether the foraging choices observed at the colony level arise from a modulation of individual behaviour of scouts or simply as an outcome of the physico-chemical properties of the environment.

Experimental colonies of *L. niger* were starved for 4 days before observing food recruitment towards a sugar-water food source. Each ant nest was given access to a foraging area via a diamond-shaped bridge (Fig. 1). The two branches of this bridge were identical except for the basic weight of the papers covering their surface (100 g/m² and 125 g/m²). Though paper is an artificial

C. Detrain (✉) · C. Natan
Laboratoire de biologie animale et cellulaire, CP 160/12,
Université Libre de Bruxelles, Av. F. Roosevelt 50,
1050 Brussels, Belgium
e-mail: cdetrain@ulb.ac.be
Tel.: +32-2-6504512, Fax: +32-2-6502445

J.-L. Deneubourg
Center for the Study of Non-linear Phenomena, CP 231,
Université Libre de Bruxelles, Boulevard du Triomphe,
1050 Brussels, Belgium

substrate, very different from the natural one on which ants deposit their trail, it allowed us to investigate, under controlled conditions, the impact of a chosen ecological factor on ants' foraging decisions. After the discovery of the food source, the choice of one foraging path by the ant colony clearly depended on the substrate. In the majority of food recruitments (72%, $n=32$), the path covered with the lower-weight paper was preferentially followed by more than half of foragers (Fig. 1). Small differences between substrates thus led to clear-cut choices of a foraging path by the colony. Surprisingly, this collective preference for one foraging path could not be linked to any substrate-related change in the individual behaviours of scouts or recruiting ants (Table 1). During the exploration of the experimental set-up, scouts behaved similarly over each branch of the bridge and walked at the same speed (two-tailed t -test, $t=1.67$, $df=53$, $P=0.10$). After the discovery of the food source, a similar percentage of ants were engaged in trail-laying whichever branch was followed on the bridge (two-tailed t -test on square-root arcsine transformed values, $t=0.52$, $P=0.61$). Furthermore, the same average numbers of

chemical marks were laid per trail-laying ant whatever the substrate of their foraging path (two-tailed t -test, $t=0.70$, $df=165$, $P=0.49$). Group-level decisions thus arose through self-organising processes, without the modulation of recruitment or any behavioural changes at the individual level.

Since no behavioural changes occurred among individual ants, colony choices appear to be driven by the substrate itself. Physico-chemical differences between the two substrates might alter the accessibility of the trail pheromone to foragers and ultimately lead, through recruitment amplifying processes, to the selection of one foraging path. Monte-Carlo simulations based on a previously validated trail-following model (Beckers et al. 1992a, b, 1993), were used to test this hypothesis by examining how substrate differences in the trail pheromone lifetime affect ants' collective choices (for details about the model, see caption to Fig. 2). The trail lifetime value used in the model stands for the time during which the trail pheromone is actually perceived by the individual ants. This functional time parameter reflects both the perceptive abilities of ants and the accessibility of the trail pheromone depending on its physico-chemical interactions with the substrate. Since it is known that the pheromone lifetime for *L. niger* is approximately 2,400 s on the lightweight paper (Beckers et al. 1993), we obtained a theoretical selection rate of this path (expected selection rate of 73%; Fig. 2) similar to the experimental value (observed selection rate of 72%; Fig. 1) by assuming, in our simulations, a trail pheromone lifetime of 800 s (trail lifetime ratio of 0.3; Fig. 2) for the less frequently selected substrate. Theoretical simulations thus confirmed that collective choices could simply be the outcome of physico-chemical differences in the abiotic environment that altered the dynamics of trail pheromone accessibility to the ants. The observed collective choices of a foraging path do not result from the simple summation of individual decisions in which each ant is more likely to perceive the trail on the lightweight paper; in this case, all the colonies would have selected the lightweight substrate with always more than 50% of ants following this path. However, in both experiments and simulations, collective choices were not so unanimous, since several colonies (around 28%) chose the heavy-weight substrate. These "unexpected" choices signify a self-organised process in which "errors" or less likely decisions taken at the individual level are amplified by

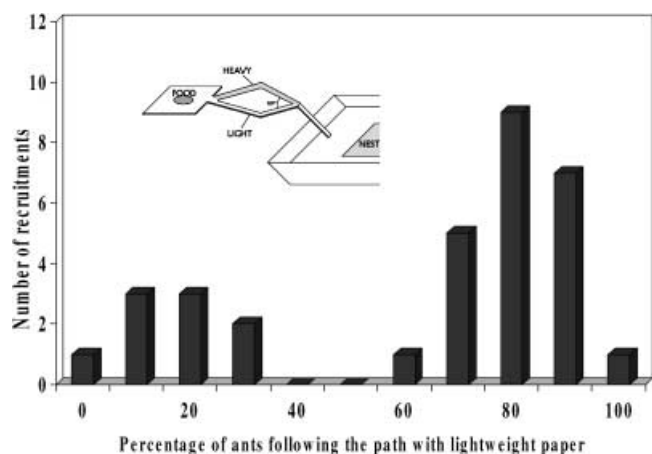


Fig. 1 Collective choices of a foraging path by *Lasius niger* ants. Distribution of food recruitments ($n=32$) as a function of path selection expressed as the percentage of all of the ants traversing the bridge that chose the lightweight paper (x axis). Between minutes 20 and 30 of each recruitment to a 1 M sucrose solution, the flow of ants was quantified on each of the two branches of the experimental set-up (upper left corner). Both branches were similar except for the type of paper covering the path (lightweight, 100 g/m²; heavyweight, 125 g/m²)

Table 1 Individual behaviour of ants on different foraging substrates. The running speed was measured before the start of food recruitment, on 30 randomly chosen ants. The percentage of trail-laying ants was calculated over the total ant traverses observed during the first 20 min of recruitment (17 recruitments observed).

	Running speed (cm/s)	Percentage of trail-laying ants (%)	Trail-laying intensity (number of marks)
Heavyweight paper substrate	2.3±0.7 ($n=30$)	37.5±16 ($n=17$)	1.63±0.87 ($n=35$)
Lightweight paper substrate	2.1±0.5 ($n=30$)	34±17 ($n=17$)	1.74±0.81 ($n=125$)

The intensity of trail-laying behaviour was compared between substrates by measuring the number of marks laid per trail-laying ant over a 7 cm section centred on each branch (observation on video recordings magnified 10×). Means ± SD for all data

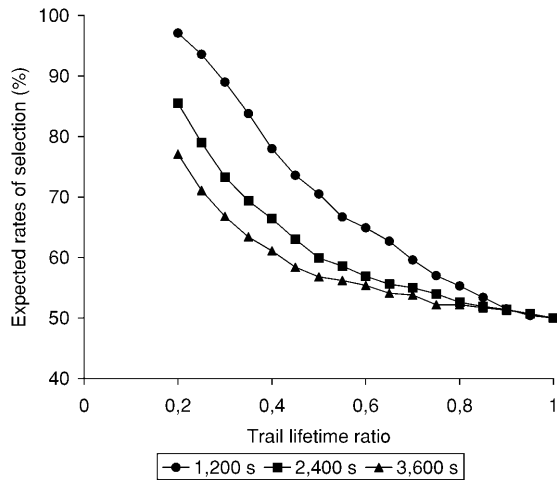


Fig. 2 Expected rates of selection of a foraging substrate. The y axis shows the selection rate of the foraging path covered with lightweight paper resulting from 10,000 Monte-Carlo simulations. This path is considered as selected when more than 50% of all of the ants traversing the bridge choose the “lightweight” substrate, between minutes 20 and 30 of the simulated food recruitment. The x axis indicates the ratio between the trail lifetimes on substrate *H* (heavyweight paper) and on the reference substrate *L* (lightweight paper). As far as *Lasius niger* is concerned, expected rates of path selection (filled squares) are calculated by taking a trail lifetime of 2,400 s on the reference substrate *L* (trail lifetime value drawn from Beckers et al. 1993). The two other curves account for ant species with shorter lived (1,200 s; filled circles) or longer lasting (3,600 s; filled triangles) trail pheromones on the reference substrate *L*. Simulations rely on an osmotropotactic model in which the probability (P_L) that an ant will choose the substrate *L* path is $P_L = (k + C_L)^n / [(k + C_L)^n + (k + C_H)^n]$. Each ant has a probability of choosing one path, which depends partly on the amount of trail laid by the ants (C). C_H and C_L are the trail concentrations on paths covered with heavy- and lightweight paper, respectively. The constant k stands for any factors other than trail, which may influence the choice of a path (e.g. thigmotactic orientation). The constant n value accounts for the sensitivity of ant choices to changes in the amount of trail pheromone laid on each path. The input flow of foragers linearly increased during the first 20 min and remained constant during the last 10 min at a plateau value determined by the experimental distribution of the ants’ flow. The following parameters were fixed equal to values drawn from experiments on *L. niger* (Beckers et al. 1993): $k=6$; $n=2$, travel time on the branch is 10 s

positive feedbacks such as trail recruitment and thus lead, at the collective level, to the selection of the substrate with a shorter trail lifetime.

The influence exerted by the substrate on the collective decision-making process was also expected to vary among ant species according to the longevity of their foraging trails. Indeed, for a given trail lifetime ratio, ant species laying short-lived trails (Fig. 2; 1,200 s curve) always showed higher rates of path selection (and consequently a higher sensitivity to the substrate) than ants following longer lasting chemical marks (Fig. 2; 3,600 s curve).

The impact of the environment on collective foraging patterns is often intimately coupled with changes in the behaviour of individual ants, as in the case of ambient temperature (Traniello et al. 1984; Marsh 1985)

which influences activity level, running speed, and searching behaviour of individual workers. Our results cast new light on environmental factors such as the substrate, which determine collective choices of ant societies, without altering behaviour or acting as a constraint at the individual level. Indeed, the abiotic environment can directly contribute to collective decision-making by determining, through its physico-chemical properties, the dynamics of information transfer by chemical trails. This can also apply to other information-laden signals, such as vibrations produced by stridulating ants, where the recruitment range might depend on the resonance properties of the substrate (Baroni-Urbani et al 1988). Although the individual behaviour of recruiting workers remains the cornerstone on which most foraging strategies are built, some collective decisions can arise automatically as a result of the dynamic properties between the ant pheromones and the abiotic environment, including the foraging substrate. Through evolution, pheromones have been selected for as an adaptation to the environment (Therrien et al 1986; Beugnon and Dejean 1992) which, together with simple individual decisions of foragers and self-organising processes, has shaped the group-level behaviour of ant societies.

Acknowledgements We thank J.M. Pasteels, N.R. Franks, as well as anonymous referees, for their critical reading of the paper. C. Detrain and J.-L. Deneubourg are research associates of the Belgian National Foundation for Scientific Research. The experiments described here comply with current European laws.

References

- Acosta FJ, Lopez FL, Serrano JM (1995) Dispersed versus central-place foraging: intra- and intercolonial competition in the strategy of trunk trail arrangement of a harvester ant. *Am Nat* 145:389–411
- Baroni-Urbani C, Buser MW, Schillinger E (1988) Substrate vibration during recruitment in ant social organization. *Insectes Soc* 35:241–250
- Beckers R, Deneubourg J-L, Goss S (1992a) Trail laying behaviour during food recruitment in the ant *Lasius niger* (L.). *Insectes Soc* 39:59–72
- Beckers R, Deneubourg J-L, Goss S (1992b) Trails and U-turns in the selection of a path by the ant *Lasius niger*. *J Theor Biol* 159:397–415
- Beckers R, Deneubourg J-L, Goss S (1993) Modulation of trail laying in the ant *Lasius niger* (Hymenoptera: Formicidae) and its role in the collective selection of a food source. *J Insect Behav* 6:751–759
- Bernstein R (1975) Foraging strategies of ants in response to variable food density. *Ecology* 56:213–219
- Beugnon G, Dejean A (1992) Adaptive properties of the chemical trail system of the African weaver ant *Oecophylla longinoda* Latreille (Hymenoptera, Formicidae, Formicinae). *Insectes Soc* 39:341–346
- Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E (2001) Self-organization in biological systems. Princeton University Press, Princeton, N.J.
- Deneubourg J-L, Goss S (1989) Collective patterns and decision-making. *Ethol Ecol Evol* 1:295–311
- Deneubourg J-L, Goss S, Franks N, Pasteels JM (1989) The blind leading the blind: modelling chemically mediated army ant raid patterns. *J Insect Behav* 2:719–725

- Deneubourg J-L, Aron S, Pasteels JM (1990) The self-organizing exploratory pattern of the Argentine ant. *J Insect Behav* 3:159–168
- Deneubourg J-L, Goss S, Franks N, Sendova-Franks A, Detrain C, Chrétien L (1991) The dynamics of collective sorting robot-like ants and ant-like robots. In: Meyer JA, Wilson S (eds) *From animals to animats*. MIT Press, Cambridge, Mass., pp 356–365
- Detrain C, Deneubourg J-L (1997) Scavenging by *Pheidole pallidula*: a key for understanding decision-making systems in ants. *Anim Behav* 53:537–547
- Detrain C, Deneubourg J-L, Goss S, Quinet Y (1991) Dynamics of collective exploration in the ant *Pheidole pallidula*. *Psyche* 92:21–31
- Detrain C, Deneubourg J-L, Pasteels JM (1999) Decision-making in foraging by social insects. In: Detrain C, Deneubourg J-L, Pasteels JM (eds) *Information processing in social insects*. Birkhauser, Basel, pp 331–354
- Franks N, Gomez N, Goss S, Deneubourg J-L (1991) The blind leading the blind in army ant raid patterns: testing a model of self-organization. *J Insect Behav* 4:583–607
- Hahn M, Maschwitz U (1985). Foraging strategies and recruitment behaviour in the European harvester ant *Messor rufitarsis*. *Oecologia* 68:45–51
- Hölldobler B (1976) Recruitment behavior, home range orientation and territoriality in harvester ants, *Pogonomyrmex*. *Behav Ecol Sociobiol* 1:3–44
- Hölldobler B, Wilson EO (1990) *The ants*. Springer, Berlin Heidelberg New York
- Hunt JH (1983) Foraging and morphology in ants: the role of vertebrate predators as agents of natural selection. In: Jaisson P (ed) *Social insects in the tropics*. University Paris Nord, Paris, pp 83–104
- Mailleux AC, Deneubourg J-L, Detrain C (2000) Do ants assess food volumes? *Anim Behav* 59:1061–1069
- Marsh AC (1985) Microclimatic factors influencing foraging patterns and success of the thermophilic desert ant, *Ocymyrmex barbiger*. *Insectes Soc* 32:286–296
- Millor J, Pham-Delgue M, Deneubourg J-L, Camazine S (1999) Self-organized defensive behavior in honeybees. *Proc Natl Acad Sci USA* 96:12611–12615
- Nonacs P, Dill LM (1988) Foraging response of the ant *Lasius pallitarsis* to food sources with associated mortality risk. *Insectes Soc* 35:293–303
- Rissing SW, Wheeler J (1976) Foraging responses of *Veromessor pergandei* to changes in seed production. *Pan-Pac Entomol* 52:63–72
- Seeley TD (1995) *The wisdom of the hive: the social physiology of honey bee colonies*. Harvard University Press, Cambridge, Mass.
- Stickland TR, Tofts C, Franks NR (1993) Algorithms for ant foraging. *Naturwissenschaften* 80:427–430
- Therrien P, McNeil JN, Wellington WG, Febvay G (1986) Ecological studies of the leaf-cutting ant, *Acromyrmex octospinosus*, in Guadeloupe. In: Lofgren C, Vander Meer RK (eds) *Fire ants and leaf-cutting ants: biology and management*. Westview, Boulder, Colo., pp 173–183
- Traniello JF, Robson SK (1995) Trail and territorial communication in social insects. In: Bell WJ, Cardé R (eds) *The chemical ecology of insects*, vol II. Chapman and Hall, London, pp 241–246
- Traniello JF, Fujita MS, Bowen RV (1984) Ant foraging behavior: ambient temperature affects prey selection. *Behav Ecol Sociobiol* 15:65–68
- Visscher PK, Camazine S (1999) Collective decisions and cognition in bees. *Nature* 397:40