

Self-organized asymmetries in ant foraging: a functional response to food type and colony needs

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The dominant paradigm to explain asymmetries in the spatial distribution of foraging animals is that they track the spatial heterogeneity of their environment. However, in social insects, endogenous spatial asymmetries can emerge within a uniform environment as an outcome from the self-organizing process of trail recruitment. We studied how self-organized asymmetries contribute to the exploitation of different food sources (carbohydrate or proteins) in colonies of the aphid-tending ant *Lasius niger* varying in their nutritional needs (presence or absence of brood). Colonies with brood fed on sucrose sources exhibit a higher mobilization of foragers than the other experimental groups. Foraging patterns differ greatly according to food type: colonies strongly focus their activity on only one droplet of sucrose, whereas they show a rather homogeneous distribution of foragers between proteinaceous sources. In addition, the presence of brood in the colony enhances the asymmetry of collective foraging for both types of food. These spatial differences in self-organized foraging patterns allow efficient exploitation of natural resources and play a role in the competitive strategy of this widespread palearctic ant. *Key words*: aphid-tending ants, brood, diet, foraging ecology, *Lasius niger*, recruitment, spatial distribution. [*Behav Ecol* 13:776–781 (2002)]

The demography and reproductive success (Boinski and Garber, 2000) of group-living animals is intimately related to their ability to discover, exploit, and defend food resources. Foraging efficiency is achieved by a shaping of the spatial distribution of animals according to food opportunities and environmental constraints within the foraged areas. As a general rule, central-place foragers such as eusocial insects do not evenly operate in all sectors around their nest but instead exhibit asymmetries in the use of their foraging space. These heterogeneities in the spatial distribution of foragers often reflect the heterogeneities of the environment such as the spatio-temporal availability of food resources (e.g., Gordon, 1991; Hahn and Maschwitz, 1985; Hölldobler, 1976) or the presence of competitors (e.g., Brown and Gordon, 2000; Gordon, 1991; Hölldobler and Lumsden, 1980).

In social organisms like ants, asymmetrical distribution of workers can emerge within a uniform environment, as demonstrated by theoretical and experimental studies (Beckers et al., 1992; Detrain et al., 1991; Franks et al., 1991; Goss and Deneubourg, 1989; Pasteels et al., 1987). These endogenous spatial asymmetries are the result of a self-organizing process, in which the foraging activity of workers is influenced by positive feedbacks such as trail recruitment. The contribution of such endogenous asymmetries to the global allocation of workers between foraging sectors remains largely unexplored. Indeed, many studies about foraging patterns of ants (Crist and Haefner, 1994; Gordon, 1991; Hölldobler, 1976; López et al., 1994; Traniello, 1989) implicitly or explicitly interpret the spatial distribution of foragers as the simple outcome of the spatial heterogeneity of resources, without considering the possible enhancing or counteracting effects of self-organized

asymmetries. Additionally, little is known about the key parameters used by the foragers to make decisions that can ultimately modulate their collective spatial distribution. We hypothesized that the nature of the food source discovered can provide reliable information with this regard because different types of food are expected to be exploited with different strategies.

In the present study, we examined the emergence of self-organized asymmetries in the spatial distribution of ants within a symmetrical experimental setup, and the influence of food nature (carbohydrate or proteins) and colony nutritional needs (colonies with brood or not) on the foraging dynamics and on the contribution of self-organized asymmetries to the spatial allocation of foragers. We choose to carry out experiments on the aphid-tending ant *Lasius niger* L. because it is known to exhibit self-organized patterns of foraging to sucrose sources leading to symmetry breaking (Beckers et al., 1992), and it has a mixed diet consisting in honeydew as carbohydrate supply and insects (including aphids) as a protein source (Pontin, 1961; Way, 1963).

MATERIALS AND METHODS

We collected *L. niger* colonies from earth banks in Brussels (Belgium). In the laboratory, ant societies were reared in plaster nests (Janet type, 20 × 20 × 0.5 cm) placed in arenas (50 × 38 cm) with fluon-coated borders to prevent escapes. Nest chambers were covered with a red glass plate through which the ants could be observed. Each queenless nest contained 1500–2000 workers and brood. Nests were regularly moistened and kept at a room temperature of 22 ± 3°C, 60% relative humidity with a constant photoperiod of 12 h light per day. We supplied ants with water, sucrose solution (1 M), and, three times a week, dead cockroaches (*Periplaneta americana*) and maggots (*Calliphora erythrocephala*). One month after their collection, we divided each colony into two experimental nests containing half of the original worker population. We froze mother nests for 20 min at 4°C, and then we removed

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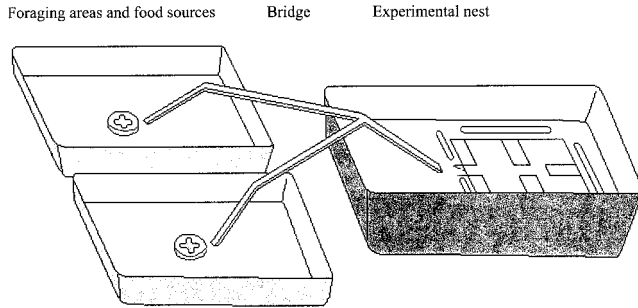


Figure 1
Experimental setup. See in the text for detailed description.

the glass plate of the nest to allow a random collection of ants from all parts of the nest. Larvae from the mother colony were transferred in one of the experimental nests (identical in shape and size to the mother nest; see Figure 1), the other one being deprived of any brood. Nests with brood contained a similar amount of larvae, which occupied 15–25% of the nest area. At least 2 weeks elapsed between the settlement of ant societies in artificial nests and the first experiments.

Each experimental nest was connected to two distinct foraging areas (21 × 32 cm) by a Y-shaped cardboard bridge (access ramp 15 cm, horizontal branches of the Y-bridge 20 cm, access ramps to foraging areas 15 cm; see Figure 1). The angle between branches of the bridge was small enough (60°) to limit U-turns by *L. niger* ants due to their aversion to move away from the nest-source axis (Beckers et al., 1992). To prevent orientation bias due to the use of visual cues (Aron et al., 1993), we avoided any asymmetry of lighting conditions by centering light ramps above the bridge axis, and we surrounded the whole experimental design with a 50-cm high opaque enclosure.

Before each experiment, we starved colonies for 4 days by depriving them of any food but water. Each tested colony was then presented with two food sources placed on each of the foraging areas (Figure 1). We counted on video recordings the number of ants walking on each branch of the bridge during the 40 min after the discovery of food by a scout. The initial increasing phase lasted at most 20 min, then recruitments reached their plateau value. We assessed the level of foraging asymmetry by comparing flows on each branch between the 20 and 40 min of recruitments.

In this strictly symmetrical set up, food sources offered to *L. niger* colonies were either two droplets (1.5 ml each) of sucrose solution, 1 M or two droplets (1.5 ml each) of proteinaceous solution, consisting of 30 maggots (*Calliphora erythrocephala*) crushed in 5 ml of water and filtered. Food sources were similar (same size, same liquid form, etc.), with the exception of the proteinaceous or sugary nature of the food solution, which allowed us to assess the influence of the food nature *per se* on *L. niger* foraging patterns.

We carried out at least 18 repetitions for each of the 4 experimental conditions: (1) colony with brood fed with two sucrose solutions, SB; (2) colony without brood fed with two sucrose solutions, SNB; (3) colony with brood fed with two proteinaceous solutions, PB; (4) colony without brood fed with two proteinaceous solutions, PNB. We deliberately offered two identical food rewards instead of setting up a competition between a proteinaceous and a sucrose solution. Indeed, when two different food sources are simultaneously offered, the spatial allocation of foragers between sources may result from other factors than self-organized asymmetries, as, for instance, individual memory or ants' preferences for a food type. Instead, competition between identical food sources

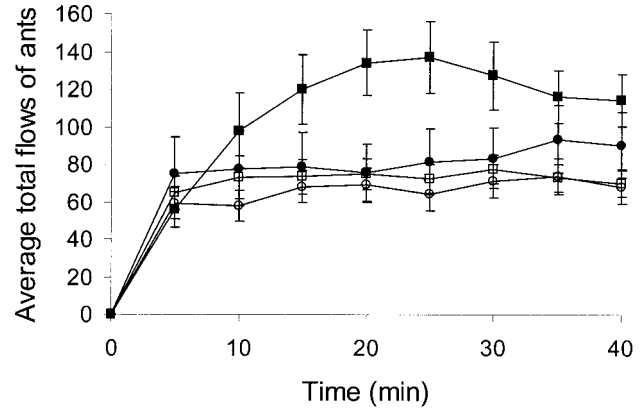


Figure 2
Time evolution of the total flows of foragers over the bridge towards sources. Flows during 5 min intervals were averaged (\pm SE) for each experimental group. Filled squares, sucrose/brood group ($n = 18$); open squares, sucrose/no brood group ($n = 20$); filled circles, protein/brood group ($n = 20$); open circles, protein/no brood group ($n = 25$).

leads to collective decisions and foraging patterns in which the chemical mass recruitment is the only decision process involved.

RESULTS

For all experimental groups, recruitment occurred (Figure 2): the number of ants walking on the bridge steeply increased during the 5 min after the food discovery. When sugary food sources were offered to a colony with brood, the increasing phase of recruitment was prolonged and lasted 20 min. At the plateau, the total flow of ants on the bridge between 20 and 40 min differed significantly between experimental groups (ANOVA $F_{3,79} = 4.372$, $p = .007$). Nests with brood fed with sucrose solutions reached significantly higher total flows of foragers (mean \pm SD = 495 ± 235 ants/20 min) than broodless nests recruiting either to sucrose (mean \pm SD = 292 ± 124 ants/20 min, Tukey test $p = .027$ for SB vs. SNB) or to proteins (mean \pm SD = 264 ± 145 ants/20 min, Tukey test, $p = .005$ for SB vs. PNB). The flow of foragers from nests with brood to proteins (mean \pm SD = 348 ± 302 ants/20 min) was intermediate and did not statistically differ from flows to sucrose (Tukey test, $p > .1$ for SB vs. PB) or from broodless conditions (Tukey test, $p > .5$ for PB vs. PNB; $p > .8$ for PB vs. SNB). *L. niger* colonies thus increased their foraging effort toward sucrose when they had to care for brood, but data did not allow us to draw conclusions concerning proteins.

For each recruitment in each experimental group, we tested for the randomness of ants' distribution over the two branches of the bridge. We arbitrarily assumed that a branch was selected and that a bifurcation occurred when the binomial test showed a significantly higher number of foragers following that branch (.05 level of significance). The percentage of experiments in which asymmetry emerged significantly differed between the four groups ($p < .001$; Table 1). For sugary food sources, selection of one branch occurred for nearly all experiments, in the presence of brood or not. When colonies were fed on proteinaceous sources, the situation was different: for nests containing brood, the rate of selection remained high (80%), but it dropped off dramatically for broodless nests (44%; Table 1). The emergence of spatial asymmetry can thus be enhanced by the presence of brood, as shown to proteinaceous food sources.

The asymmetry level—that is, the averaged ratios of ants

Table 1
Percentage of selection of a food source and asymmetry level

	Rate of selection	Asymmetry level	<i>n</i>
Sucrose/brood	100%	0.92 ± 0.08 ^a	18
Sucrose/no brood	90%	0.78 ± 0.13 ^b	20
Protein/brood	80%	0.72 ± 0.14 ^b	20
Protein/no brood	44%	0.59 ± 0.07 ^c	25
Statistical tests	$\chi^2 = 22.01, p < .001$	ANOVA $F_{3,79} = 39.912, p < .001$	

The rate of selection is given by the percentage of experiments in which one food source was selected. For each experiment, a food source was considered as selected when the corresponding branch carried a significantly different number of foragers (binomial test, .05 level of significance). For each experiment the asymmetry level is given by the ratio between the flow of ants walking on the winning branch over the total flow of foragers from 20 to 40 min. The asymmetry levels were averaged (\pm SD) and tested by one-way ANOVA, followed by multiple comparisons using post-hoc Tukey test (.05 level of significance). Groups sharing the same letter are not statistically different.

walking on the winning branch of the bridge—also differed between groups ($p < .001$; Table 1). This ratio can vary from 0.5 when the two food sources were equally exploited to 1 when ants exclusively followed one branch of the bridge. Ants fed with sucrose strongly selected one of the two food sources, whereas both sources tended to be exploited equally when they consisted of maggot juice (post-hoc Tukey test comparisons between sucrose and protein when considering either colonies with brood: $p < .001$ for SB vs. PB; or colonies without brood: $p < .001$ for SNB vs. PNB). The presence of brood within the nest enhanced the asymmetry of spatial allocation of foragers to a given food reward: the asymmetry level was 15% higher than for broodless nests to sucrose sources (post-hoc Tukey test $p = .001$ for SB vs. SNB), and 18% higher to maggot juice (post-hoc Tukey test $p < .001$ for PB vs. PNB).

Due to the autocatalytic nature of trail recruitment (Pasteels et al., 1987), the emergence of symmetry breaking is sensitive to the number of foragers. In our experiments, however, the total flow of ants on the bridge and the asymmetry level were never correlated ($r^2 = .038$ for SB group, $r^2 = .032$ for SNB group, $r^2 = .146$ for PB group, $r^2 = .005$ for PNB group, and $r^2 = .041$ for pooled data, all ns). This suggests that (1) these flows were always above the critical numbers of ants needed for the emergence of asymmetry, and (2) variations in ant flows were not responsible for the observed variations in asymmetry level within each experimental group (Table 1). Moreover, because PNB, PB, and SNB groups exhibited similar ant flows (see above and Figure 2), between-group increases in asymmetry levels (Table 1) could not result from larger numbers of recruited foragers, but should rather result from increase in the intensities of trail-laying behavior. Similarly, increased trail-laying behavior should be assumed to account for the very strong asymmetry level observed for recruitments of the SB group (9 over 18), in which the flows were of the same order of magnitude than in the other groups.

For each group we drew the distribution of the relative frequencies of experiments as a function of the ant traffic on the right branch (Figure 3). In our symmetrical setup, the pattern of ants' distribution between the two food sources is also informative about the recruitment process: it is a highly sensitive means to detect and to visualize differences in recruitment rates and/or trail-laying behavior. The ratio of experiments in which the left branch was selected (i.e., took more than 50% of the total ant flow) never differed from random. Because there was no orientation bias in path selection in our symmetrical setup, asymmetries in spatial allocation of foragers relied exclusively on differences in trail recruitment between groups.

When sucrose sources were offered to nests with brood (Figure 3a), the distribution was U-shaped and showed a clear-cut selection of one source, suggesting a strong amplifying mechanism of recruitment. SNB (Figure 3b) and PB (Figure 3c) groups had similar distributions with a more uniform shape: asymmetry level is smaller than for SB group, and asymmetry failed to emerge in several experiments (2 over 20 and 4 over 20 respectively). In the PNB group (Figure 3d), no strong asymmetry of flow ratios occurred, and experiments with 0.4–0.6 flow ratios made up the core of the distribution (17 over 25). This does not imply that foragers of the PNB group chose their path at random because a slight amplification process might be involved, as validated by computer simulations of random path choices. A theoretical distribution was drawn from those simulations in which individuals chose their path at random (following binomial law with $p = q = 0.5$) and in which the numbers of choosing foragers were equal to the experimental ant flows in PNB recruitments. The theoretical occurrence of experiments with 0.4–0.6 flow ratios was expected to be 0.993 if ants were choosing path at random. Because this expected value is significantly higher than the observed occurrence (0.680; $\chi^2 = 196.92, p < .0001$), we should assume that trail recruitment of weak intensity occurred in the PNB group.

DISCUSSION

In mass-recruiting ant species like *L. niger*, foraging patterns mainly rely on chemical trails, which act as stimulating signals, increasing emergence of nest mates from the nest (recruitment effect) as well as orientation cues channeling them to feeding areas (orientation effect). The relative amount of pheromones at each branching point of trails determines the distribution of foragers between the foraging sectors. Due to the snowball effect of trail communication, symmetry breakings (in which one source is more exploited than the other) are more likely to occur for stronger chemical trails (Pasteels et al., 1987). In broodless nests of *L. niger*, the spatial allocation of foragers markedly differed according to food quality: ants were evenly distributed on the two proteinaceous food rewards, but they showed marked choices of one food source in the presence of sucrose droplets. This suggests that the perception of carbohydrates elicit a higher trail-laying behavior than a proteinaceous food supply among foragers. The chemical nature of food can therefore govern the recruitment decisions of the foragers without them necessarily using other relevant cues, such as the solid or liquid state of the food. Sucrose is thus one key used by the ants to identify and initiate strong trail recruitment to food sources that are rich and

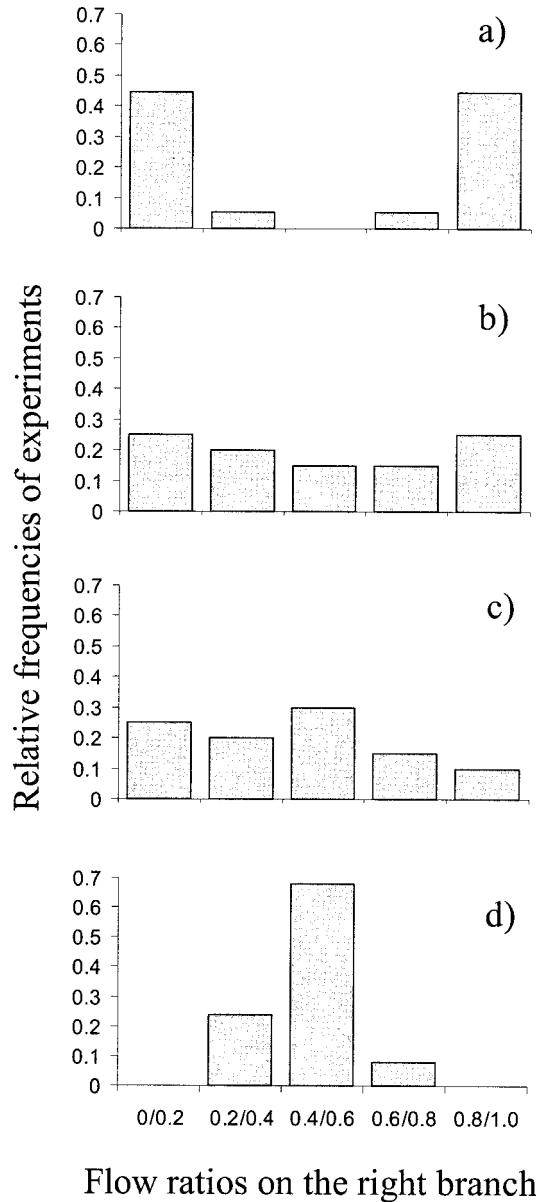


Figure 3
Percentage of experiments with between 0–100% traffic on the right branch of the bridge for each experimental series. (a) sucrose/brood ($n = 18$); (b) sucrose/no brood ($n = 20$); (c) protein/brood ($n = 25$); (d) protein/no brood ($n = 25$).

highly rewarding, such as aphid colonies. Indeed, these aphid colonies provide not only a spatially stable and renewable supply of carbohydrates (in the form of honeydew), but also amino acids (Auclair, 1963; review in Way, 1963) and proteins (namely, through predation of aphids: Fischer et al., 2001; Offenberg, 2001; Pontin, 1961; Sakata, 1994; Way, 1963).

The enhanced spatial asymmetry of workers to sucrose droplets observed in the laboratory is also consistent with the exploitation by *L. niger* of a limited number of honeydew sources in nature (Portha, personal observation). By avoiding dispersion of workers between multiple sources, the pool of foraging and defending ants is focused and maintained at the exploited aphid colonies, which provides *L. niger* with three main advantages. First, such “owner strategy” allows *L. niger* to monopolize resources that are worth defending from competitors because aphid colonies are large, renewable, and

long-lasting sources of honeydew (Blüthgen et al., 2000; Johnson and Hubbell, 1987). Second, this strategy allows *L. niger* to defend their resources efficiently against competitors, thanks to a large colony size coupled with a strong mass recruitment and the use of formic acid weaponry (Davidson, 1998; Fellers, 1987; Franks and Partridge, 1993; McGlynn, 2000; Savolainen and Vepsäläinen, 1988; Vepsäläinen and Savolainen, 1990). Finally, this spatial concentration of foragers can be a strategy of predator resistance in the sense that this small-sized ant can successfully repel predators only en masse (Hunt, 1983).

Conversely, the even distribution of foragers between artificial proteinaceous sources is consistent with the opportunistic retrieval of prey exhibited by ants in natural conditions. This strategy allows the society to maximize the discovery and intake of proteins that are scattered, scarce, and limiting (Retana et al., 1991; Schoener, 1974). Because the exploitation of a proteinaceous source never leads to a massive mobilization of ants in restricted areas, less spatial disruption occurs in scanning the whole foraging area, which maximizes the probability of discovering new preys (Deneubourg et al., 1983). Moreover, because prey are ephemeral and unpredictable items in time and space (Traniello et al., 1991; Wehner et al., 1983), there is no need to mobilize a huge foraging force for their exploitation and defense. In most cases, small groups of 5–15 cooperating ants are the most efficient means of bringing prey back to the nest (Portha, personal observation; Traniello, 1983) and can even account for 85% of the prey biomass harvested by the closely related nearctic *Lasius neoniger* (Traniello, 1983). This more dispersed and individual-based foraging strategy could be achieved by a weak trail-laying activity, resulting in poor recruitment and a low accuracy of following response.

Ant colonies also adjust their harvesting strategy to the internal demand for nutrients within the nests. Although ants need carbohydrates as a source of energy for colony maintenance, the production of new workers and reproductives relies essentially on proteins but also on sugars (Cassill and Tschinkel, 1999; Sorensen and Vinson, 1981). Food recruitment and foraging patterns are therefore expected to track colony demography and larval growth. The presence of brood in the colony increases the mobilization of foragers as well as the level of symmetry breaks when ants feed at sucrose droplets, probably through a stronger trail-laying behavior. This higher level of cooperation between foragers improves the exploitation and the monopolization of carbohydrate sources that help the colony meet the energy requirements of larvae.

The influence of brood is somewhat different when ants are faced with proteinaceous droplets: the asymmetry of food exploitation, and the related trail intensity, increases in the presence of brood, but the global flows of foragers remain unchanged. The increased demand for nutrients by larvae thus influences trail intensity but does not alter the pool of workers mobilized for retrieval of proteinaceous food. Two nonexclusive mechanisms can explain this phenomenon. First, the recruitment effect of the trail (here, assessed by the number of exiting ants) could be not linearly related to the amount of laid pheromone (Van Vorhis Key et al., 1981). The brood-related increase in trail strength toward proteins might fall within a range of concentration that influences the orientation response of ants at trail bifurcation points, but that does not alter the trail recruitment effect. A second possible explanation is that only a subgroup of ants are specialized in foraging proteinaceous resources. Such a specialization for a given food type is a widespread feature among ants within the Formicinae subfamily (Higashi, 1978; Quinet and Pasteels, 1996; Sundström, 1993; Traniello et al., 1991; Wehner et al., 1983) but remains to be demonstrated in the *L. niger* species.

If we assume that the number of foragers allocated to each food type reflects the nutritional needs of the colony (Fowler, 1993), then carbohydrates account for most of *L. niger* diet, as in most exudate-feeding ant species (Alsina et al., 1988; Hennaut-Riche et al., 1979; Retana et al., 1988; Rosengren and Sundström, 1991). By relying on a food supply such as honeydew that is close to the base of the trophic pyramid, because it is derived from plant sap, ants like *L. niger* can maintain larger colonies than would be possible if they were mostly feeding on animal matter (Tobin, 1994). Moreover, carbohydrates obtained in excess of those used with proteins for colony growth can be directed toward high-tempo activity and aggressiveness, maintenance and defense of territories, and investment in nitrogen-free chemicals, weaponry (Bergström and Löfquist, 1970; Billen and Morgan, 1998), and exoskeleton (Davidson, 1997, 1998; Tobin, 1994).

An important next step would be to understand (1) how individual scouts convey the information about food quality to nest mates, (2) how information about colony needs reach the foragers, and (3) how the collective patterns observed emerge from the modulation of foragers' behavior by this information. Work is in progress to ascertain the relative importance of trail-laying behavior, individual memory, specialization, invitation displays, and food transfers in the recruitment process toward food sources differing in quality.

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