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Modulation of individual behavior and collective decision-making during aggregation site selection by the ant *Messor barbarus*

Abstract Insect societies are often confronted with choices among several options such as food sources of different richness or potential nest sites with different qualities. The mechanisms by which a colony as a whole evaluates these situations and takes the appropriate decision are of crucial importance for its survival. Here we studied how collective decisions arise from individual behaviors when a group of workers of the ant *Messor barbarus* is given a choice between two aggregation sites. Two hundred ants were introduced into an arena and given a choice between two tubes connected to the arena. The tubes had different physical properties: dry and transparent (termed as dry), humid and transparent (termed as humid), or dry and dark (termed as dark). After 30 min, most ants were found to be aggregated in a humid tube when paired with a dry tube, or in a dark tube when paired with a humid one. When two humid tubes were in competition, ants aggregate more in one of the sites. The choice of ants was consistent throughout experiments. An analysis of individual behaviors shows that the probability of an ant recruiting and the intensity of its trail-laying behavior strongly depend on the quality of the tubes. Our study suggests that the selection of an aggregation site does not require that individual ants directly compare sites, but rather relies on the synergy between amplification processes involving recruitment by chemical trails, and a modulation of the individual resting time in a site as a function of its population.

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Introduction

In insect societies, many cooperative tasks lead to collective decisions that rely on interactions taking place between individuals following simple rules and having access only to local information (Camazine et al. 2001). Collective decisions occur when a colony is faced with several opportunities, such as food sources or potential nest sites, each of them having different qualities. Information about these opportunities is gathered by individual scouts and brought back to the nest where it is shared with nestmates. The by-product of this distributed processing is a collective choice of one of the opportunities (Franks et al. 2002). While no individual is aware of all the alternatives, the colony as a whole reaches a consensus, and focuses its foraging activity on the richer food source or chooses the best available nest site. This raises the question of the mechanisms allowing the colony to achieve a decision when faced with several alternatives.

In social insects, a key element underlying such decision-making processes takes the form of positive feedbacks that are implemented at the individual level through a behavioral modulation in two different ways. One way involves a modulation of individual behavior without any active information transfer between nestmates. This occurs, for instance, during chain formation in the ant *Oecophylla longinoda* or during the selection of a common shelter in groups of cockroaches *Blattella germanica*. In both cases, the time an individual remains inside the chain or the shelter increases as a function of the number of conspecifics already present in the place, leading to the choice of a unique site through an amplification process (Rivault and Cloarec 1998; Lioni et al. 2001; Deneubourg et al. 2002; Amé et al. 2003). The other way for positive feedback to be implemented at the individual level involves the active transmission of

information among individuals through, for instance, the use of pheromone trails in ants (Hölldobler and Wilson 1990) or waggle dances in bees (Seeley 1995). The use of signals is a particularly convenient way to inform nestmates about the qualities of a distant resource.

In order to achieve a decision when faced with several alternatives, bees and ants should assess the profitability of food sources (Beckers et al. 1990, 1992, 1993; Seeley et al. 1991; Seeley 1995; Mailleux et al. 2000) and the suitability of potential nest sites (Seeley 1977, 1982; Seeley and Morse 1978; Seeley and Buhrman 1999; Visscher and Camazine 1999; Mallon and Franks 2000; Mallon et al. 2001; Mugford et al. 2001; Pratt et al. 2002; Franks et al. 2003). Depending on their perception of the resource quality, individuals adjust the intensity of the signal conveyed. For example, bees modulate the strength of the waggle dance in accordance with the suitability of a potential nest site or the profitability of the food source (Seeley et al. 2000; Seeley and Buhrman 2001). During foraging, ants modulate the intensity and frequency of trail-laying in relation to the concentration of the food sources (Beckers et al. 1992).

In the context of house-hunting in ants, the decision relative to the selection of a potential nest site has been mainly investigated in species using tandem running, such as *Leptothorax albipennis* where the collective decision-making results from a modulation of the ant's probability of initiating a recruitment depending on the site suitability: the better the quality of the site, the shorter the latency between discovery and recruitment to this site (Mallon et al. 2001; Franks et al. 2002, 2003). In ant species using mass communication, less attention has been paid to the individual behaviors leading to a collective decision, with the exception of foraging. One should examine whether the information relative to the qualities of a potential nest site could be conveyed through the chemical trail laid by workers and, if so, whether the signal production is modulated depending on the shelter properties. In this paper, we study how collective decisions arise in the Mediterranean ant *Messor barbarus*, when a group of workers is faced with the choice between two potential aggregation sites with identical or different qualities. Although such an experimental situation appears artificial compared to natural conditions, it nevertheless offers the controlled laboratory settings required to carefully investigate the individual behavior, and is a first step to understanding the mechanisms involved during nest-moving in trail-laying ants. At the group level, we asked whether ants are able to select an aggregation site and how the choice was affected by the site properties. We then quantified individual behaviors, with particular attention being paid to testing whether workers adjust the intensity of their recruitment through a modulation of their trail-laying behaviors. Finally, we investigated the underlying mechanisms leading to the stabilization of the ants in the selected place.

Methods

Study organism

We worked on the harvester ant *Messor barbarus* which lives in monogynous colonies of about 8,000 individuals (Cerdan 1989). In sandy grounds, these ants dig nests composed of a network of galleries with interconnecting chambers containing brood, workers and seeds. A previous study has shown that *M. barbarus* uses mass communication, i.e. chemical trails alone can elicit recruitment (Heredia and Detrain 2000). Experiments were carried out on two queenless colonies collected near Narbonne, France. Each colony had a worker population of around 5,000 workers and was housed in glass tubes (length: 21 cm; ∅: 2 cm) with a damp wad of cotton at the end. The tubes were covered by black paper and placed in two connected plastic trays (45×35×10 cm), the walls of which had been coated with Fluon to prevent the ants from escaping. The colonies were reared in a room with a 12:12 light-dark cycle. The room temperature was kept at 25±2°C with a relative humidity of 40%. Colonies had permanent access to water and mixed seeds and they were fed three times a week with freshly cut mealworms and vitamin-enriched food (Bhatkar and Withcomb 1970).

Collective behavior

For the experiments, we used a 50-cm-diameter circular arena whose wall was coated with Fluon. The floor of the arena was a white PVC plate. Two apertures in the wall of the arena gave access to 1.3-cm-wide and 14-cm-long plastic tubes, each of which could easily contain more than 200 ants (Fig. 1a). Before the beginning of an experiment, the tube entrances were sealed with adhesive tape to prevent the ants from entering the tubes. Two hundred ants were then collected in nest tubes and placed into the arena. A slightly shady area located on the opposite side of the tube entrances attracted the ants to aggregate close to the wall of the arena, at an equal distance from the potential aggregation tubes. After a period of time that ranged from 90 to 120 min, at least 75% of the ants were aggregated. If the aggregate was located at equal distances from both entrances, both tubes were gently opened simultaneously. Otherwise the experiment was interrupted. The events during the next 30 min were then recorded with a digital video camera (Sony CDR-VX 2000 E) placed above the arena.

Three kinds of tubes with different properties were used in binary choice experiments: dry and transparent tubes with the bottom filled with dry cotton, humid and transparent tubes with the bottom filled with damp cotton, or dry and dark tubes surrounded
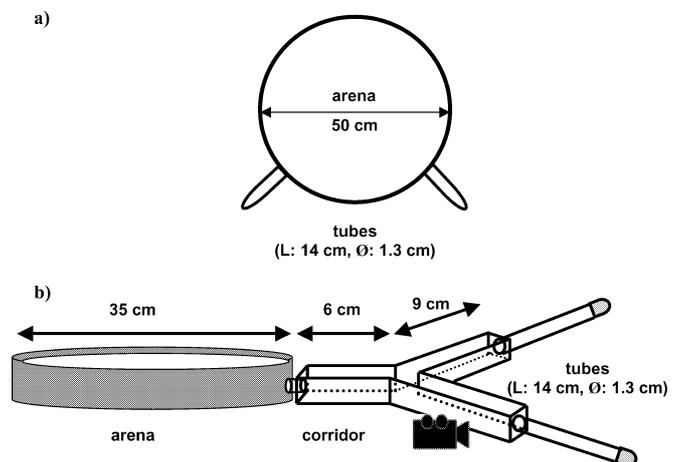
Fig. 1a,b Experimental set-up designed for **a** collective and **b** individual behaviors

by thick black paper. These tubes will be referred to hereafter, respectively, as dry, humid and dark. All tubes had exactly the same shape, length and volume and their relative positions were randomized so as to eliminate any directional biases. Ants were offered binary choices between a dry and a humid tube, a humid and a dark tube and two humid tubes. Thirteen replications were made for the first two situations and 14 replications of the last one. After each replication, the PVC plate was cleaned with hot soapy water and alcohol. The binary choice experiments involving two humid tubes were performed to study the influence of amplification in the decision-making process. If such an amplification process occurs, we would expect that a majority of ants would chose one tube instead of being equally distributed on both sites. These experiments were not designed to rank colony performance according to an exhaustive combination of the physical properties of the tubes. Furthermore, three combinations of two discrete attributes (transparent vs dark, dry vs humid) were chosen to give ants a choice between sites characterized by differences in their attractivity. Thus, these sites were expected to induce a clear choice at the collective level, as well as the opportunity to measure any behavioral differences at the individual level.

To deduce the global dynamics of the binary choice, we measured the flows of individual ants coming into and leaving each tube every 5 s during the 1st 12 min (with the exception of one replication in which it was measured for 30 min) after the ants had been given access to the tubes. This was repeated five times with a dry versus humid tube, eight times with two humid tubes and six times with a humid versus dark tube. After 30 min, we counted the number of ants that were gathered in each tube for each replication and for the three kinds of binary choices. For each replication, we determined whether ants significantly chose one site over the other by comparing the number of ants gathered in each tube with a binomial test. For each kind of binary choice, we determined whether the choices made by the ants were consistent through the replications and which type of tube was preferred by the ants, with a Wilcoxon paired-sample test (when two humid tubes were involved, the comparison was performed between the tubes gathering the smallest and the highest population of ants).

Individual behaviors

Our aim was to determine how the quality of the tube affected the individual probability of recruiting nestmates towards the site discovered. We compared for each kind of tube the latencies from the moment a scout entered a tube until she left the tube. However, the estimation of the latencies relative to the tube quality may be biased because in some cases several ants can simultaneously enter the tube. To reduce the number of ants simultaneously finding a tube, we designed a slightly different experimental set-up. We used a circular arena 50 cm in diameter, in which the ants had access to six regularly spaced tubes. The procedure was similar to the one used in binary choices; when 75% of the ants were aggregated, six tubes were simultaneously opened and the behavior of the ants was recorded with a camera placed above the arena. Measures were done on the first three ants that visited a tube. Five replications were performed with two humid, two dry and two dark tubes and one replication with six dark tubes. The latencies of the ants for each type of tube were compared with a Kruskal-Wallis test.

To analyze the potential influence of a direct comparison among sites in the decision-making process, we determined whether ants that have discovered a site returned directly to the aggregate or visited the alternative site before recruiting nestmates. Thus, for each experiment performed at the collective level (see above), we determined whether the first scout that discovered a tube, either re-entered the same tube, went into the other tube or came back to the aggregate. When the scout came back to the aggregate, we computed the time between her departure from the tube and her return to the aggregate. The times to reach the aggregate collected for the three types of tubes were compared with a Kruskal-Wallis test.

To examine whether the tube properties had an influence on trail-laying behavior by ants, we designed a different experimental set-up. We used a 35-cm-diameter arena connected to a Y-shaped Perspex corridor of 15 cm length (Fig. 1b). A tube was connected at the end of each branch of the corridor. The tubes were the same as those used in binary choice experiments described above. At the beginning of an experiment, 200 ants were placed in the centre of the arena. When at least 75% of the ants were aggregated, the access to the corridor was opened. The behavior of the ants was recorded with a high-definition video camera placed on the side of the corridor. A camera (Sony Hyper HAD with a zoom lens 18–108 mm) focused on a 5.5-cm horizontal section of the corridor just before the entrance of one tube. Pilot experiments showed that observations limited to this 5.5-cm section provided a reliable estimate of the average marking over the whole length of the corridor. The positions of the tubes were randomized in each trial and the floor of the corridor was cleaned between successive trials. When ants deposit pheromones, they display a typical behavior: their abdomen is bent downward and touches the ground while they are still walking. This was taken as a criterion for trail-laying behavior (e.g. Beckers et al. 1992). For each type of tube we computed the frequency of trail-laying behavior, defined as the proportion of ants that exhibited this behavior after they came out of the tube. We also measured the intensity of trail-laying behavior, defined as the distance over which ants displayed this behavior, on the part of the branch that was filmed. From the video recordings, we measured the behaviors of the first 20–25 ants that left a dry tube paired with a humid one (6 replications), that left a humid tube paired either with a dry one (2 replications), with a humid one (3 replications) or with a dark one (3 replications), and that left a dark tube paired with a humid one (7 replications). We compared the frequency of trail-laying behavior induced by tubes of different quality with a test designed for comparing more than two proportions, followed by a post-hoc Tukey multiple comparison test (Zar 1999). The trail-laying intensities were compared with a Kruskal-Wallis test followed by a post-hoc Dunn's test (Zar 1999).

To determine how the population of nestmates already in the tube affects the individual probabilities of an ant leaving this site and whether this probability depends on tube quality, we used the data on the flow of ants entering and leaving each type of tube (see above). In order to get an accurate estimate of the probability of an ant leaving a dry tube, we performed two additional experiments in which ants were given a choice between two dry tubes. A separate experiment was necessary because a dry tube in competition with a humid one only attracts a few ants. We pooled the data for each type of tube and computed for each 5-s interval the mean number of ants in the tube and the mean number of ants leaving the tube. We then computed the fraction of leaving ants (number of leaving ants/ number of ants in the tube) as a function of the population gathered in the tube. This fraction corresponds to the mean probability of an ant leaving a tube as a function of its population. To test for differences between the three kinds of tubes, we compared the three regression lines describing the relationship between the logarithm of the fraction of leaving ants and the population of ants in the tube.

All statistical tests were two-tailed and were carried out with SPSS 11.0 for Windows, except Tukey multiple comparison tests, multiple comparison tests of slopes, and non-parametric post-hoc tests that were performed according to the procedures described in Zar (1999).

Results

Collective behavior

After a short period of time during which both tubes are equally visited, the migration towards one of the tubes increases dramatically (Fig. 2). Qualitatively, the logistic shape of the recruitment curve suggests that the selection of a tube and the migration of the ants result from a

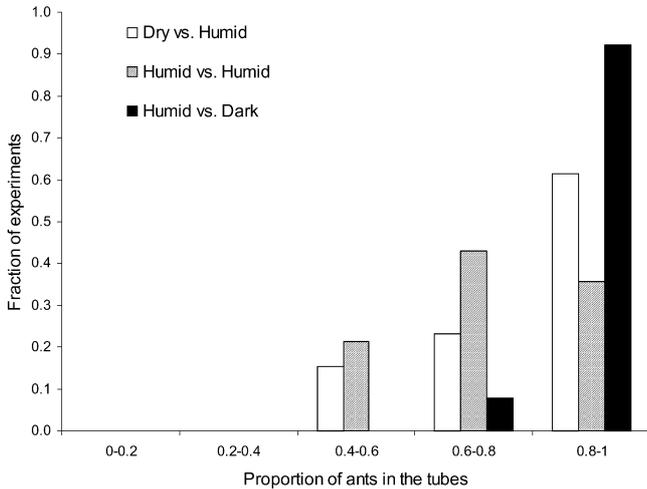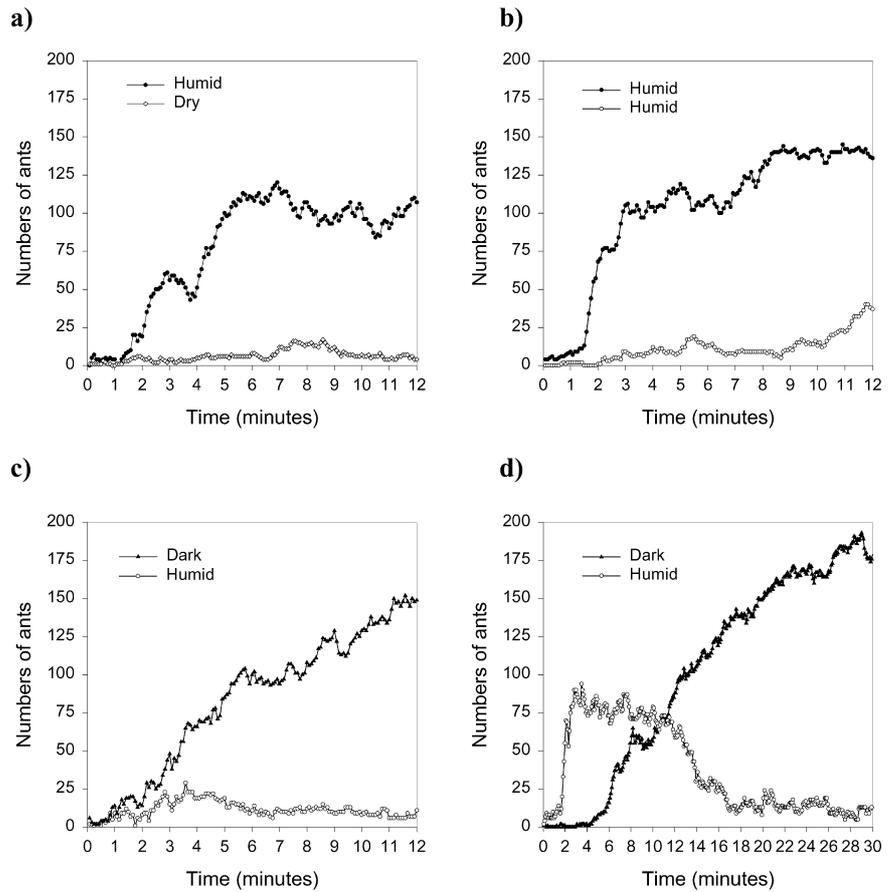**Fig. 2a–d** Examples of dynamics observed for the three binary choices studied

Fig. 3 The proportion of ants found after 30 min in the preferred tube in the binary choice experiments

Fig. 4 Mean number (±SE) of ants found after 30 min in the tubes and in the centre of the arena

positive feedback process. Eventually, the ants aggregated in one of two tubes in all but four cases (Fig. 3). There were no significant preferences for either of the two tubes in the two trials involving a dry and humid tube (binomial test: $P=0.75$ and $P=0.25$) and the two trials with two humid tubes (binomial test: $P=0.15$ and $P=1$). At 30 min,
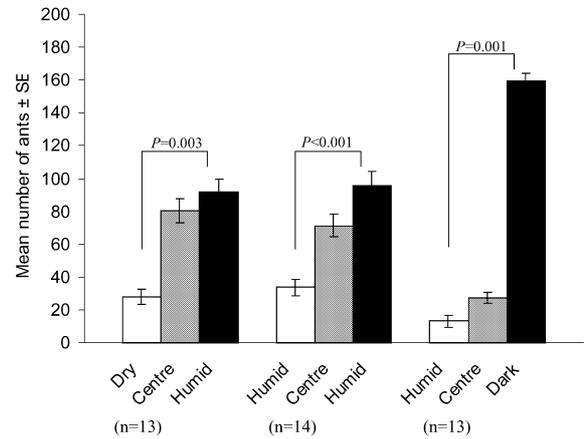
the number of ants aggregated was greater in the humid tube when paired with a dry one (Wilcoxon paired sample test: $T_{12}=-2.97$, $P=0.003$) and greater in the dark tube when paired with a humid one (Wilcoxon paired sample test: $T_{12}=-3.18$, $P=0.001$) (Fig. 4). When two humid tubes were in competition, one tube gathered more ants than the other one (Wilcoxon paired sample test: $T_{13}=-3.3$, $P<0.001$).

Table 1 Time budgets, visiting patterns and trail-laying activity among individual ants entering tubes in binary choice experiment. Values with different *letters* differ significantly; see text for detailed statistics

|		Dry	Humid	Dark	Significance
Median time spent in the tube		31 s[a] (*n*=30)	17.5 s[a, b] (*n*=26)	13.5 s[b] (*n*=36)	*P*=0.012
Behavior of the first ant that exits a tube	Number of ants that directly return to aggregate	10	46	10	
	Median time to reach aggregate	39.5 s	35 s	37.5 s	*P*=0.89
	Number of ants that visit other tube	1	2	1	
	Number of ants that re-enter tube	2	6	2	
Frequency of trail-laying±95% CI		0.32±0.08[a] (*n*=126)	0.41±0.07[a, b] (*n*=173)	0.54±0.08[b] (*n*=148)	*P*<0.005
Intensity of trail-laying (mm)±SD		10±1.72[a] (*n*=41)	12.37±1.26[a] (*n*=71)	20.52±1.9[b] (*n*=80)	*P*<0.001

Individual behaviors

The time between an ant's first entry into a tube until she left was greater in a dry tube than in a dark tube (Kruskal-Wallis test: H_2=8.80, *P*=0.012; Dunn's test: *Q*=3.48, *k*=3, 0.001<*P*<0.002) (Table 1). No differences were found in the time spent by the ants in a dry or dark tube versus the time spent in a humid tube (Dunn's test, respectively: *Q*=1.84, *k*=3, 0.1<*P*<0.2; *Q*=1.04, *k*=3, *P*>0.5).

Whatever the tube's properties, more than 80% of the ants that first discovered a tube went back to the aggregate without visiting the other tube, about 12% re-entered the tube and 5% visited the alternative tube (Table 1). There were no significant differences in the time required by the ant to reach the aggregate among the different types of tubes (Kruskal-Wallis test: H_2=0.23, *P*=0.89).

The frequency of trail-laying behavior was greater when ants came from a dark tube than when they came from a dry tube (test for comparing more than two proportions: χ^2_3=13.27, *P*<0.005; post-hoc Tukey-type multiple comparison test: *q*=5.12, *k*=3, *P*<0.001) but not when comparing dark and humid tubes (post-hoc Tukey-type multiple comparison test: *q*=3.31, *k*=3, 0.05<*P*<0.1) or dry and humid tubes (post-hoc Tukey-type multiple comparison test: dry vs humid: *q*=2.14, *k*=3, *P*>0.2) (Table 1). The intensity of trail-laying was also greater when ants came out of a dark tube than when they came out of a dry or a humid tube (Kruskal-Wallis test: H_2=18.03; *P*<0.001; non-parametric post-hoc Dunn's test: dark vs humid: *Q*=2.63, *k*=3, 0.02<*P*<0.05; dark vs dry: *Q*=4.06, *k*=3, *P*<0.001) but not when comparing dry and humid tubes (non-parametric post-hoc Dunn's test: *Q*=1.81, *k*=3, 0.2<*P*<0.5) (Table 1). Together, these results clearly indicate that ants modulate their trail-laying behavior according to the properties of the site they have just visited.

The probability of an ant leaving a tube decreases exponentially with the population of ants already in the tube (Fig. 5). The slopes (≈−0.017) of the linear regression curves correspond to the retention effect exerted by the aggregated ants in the tube. Comparison of the linear regression slopes indicates that the different tube qualities had no effect on the aggregation of ants
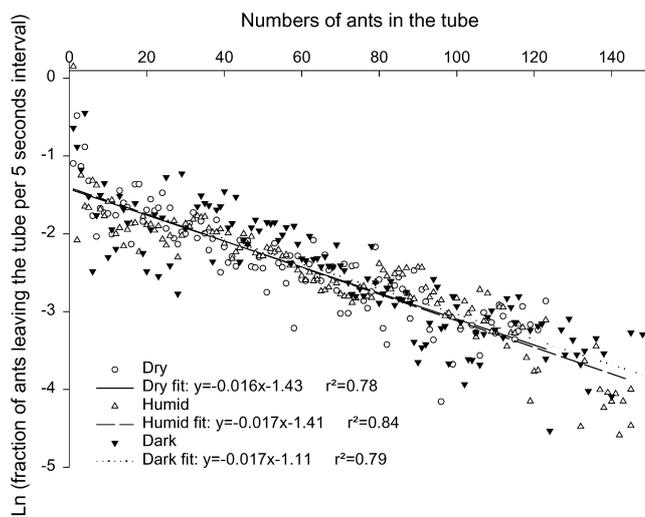
Fig. 5 Natural logarithm of the fraction of ants leaving tubes per 5-s intervals as a function of the population gathered in tube

(multiple comparison test of slopes: $F_{2,369}$=0.16, *P*>0.5) (Zar 1999).

Discussion

When offered a choice between two aggregation sites with different or identical properties, groups of *M. barbarus* ants clearly select one site. For a given pair of options, the choice made by the ants was consistent throughout the experiments: ants chose a humid tube over a dry one and a dark tube over a humid one. A direct comparison among tubes does not seem to play a role in making this decision: only 5% of the scouts that had discovered a site visited the alternative place. Rather it seems that the choice relies on positive feedback processes involving chemical trails. However, to definitely rule out the influence of direct comparison, further studies should test whether a decision still arises when comparisons are experimentally prevented. Nevertheless, we have shown that the frequency and intensity of trail-laying are modulated according to the properties of the tubes: the dark tube induces a more intense signaling than the other sites, which leads to a greater migration. To the

best of our knowledge, our work is the first evidence that ants using mass communication actively modulate their trail-laying behaviors to signal the quality of a resource in another context than foraging.

Although there were no significant differences in the intensity and frequency of trail-laying behavior or in latency times for ants coming back from the humid and dry tubes, the humid tube is chosen over the dry one (Fig. 4). Furthermore, we observed a collective choice (also called symmetry-breaking) of one site between identical options, which cannot be explained by an intrinsic difference in the rate of recruitment towards the tubes. Both phenomena are a characteristic and a consequence of an autocatalytic process, where even small variations in the rate of recruitment, due to the trail-laying and the variation of the recruitment latency for the first visiting ant, can be amplified and induce the selection of a site (Camazine et al. 2001). Such symmetry-breaking processes are a well-known outcome of a recruitment process based on chemical trails (Nicolis and Deneubourg 1999). In that sense, our results show strong similarities with those obtained during foraging in *Lasius niger*, in which even a small difference in the intensity of trail-laying, induced by an increase of food concentration, leads to the selection of the richest source (Beckers et al. 1993). This property also explains the results obtained with two identical humid tubes.

In nest-moving, this symmetry-breaking due to the trail is reinforced by aggregation processes similar to those described for the chain formation in *Oecophylla* or the shelter selection in *Blattella* (Lioni et al. 2001; Amé et al. 2003). Indeed, we have shown that the resting time in a refuge site increases with the number of workers already in this site because the greater the number of workers in a tube, the smaller the probability that an ant leaves that tube. This modulation, independent of tube qualities, plays a role in the selection of a site and acts as a mechanism leading to the cessation of the recruitment and allowing the stabilization of ants in a tube. Moreover, a mathematical analysis shows that in situations in which a direct exchange between identical resting sites occurs, without any recruitment, this aggregation process is able to produce symmetry-breaking (e.g. Amé et al. 2003). Hence, the selection of an aggregation site in *M. barbarus* appears to be the result of a combination of two positive feedbacks, the first being induced by a chemical recruitment process, and the second by an aggregation process inside a tube. This combination is essential to keep all the workers together, preventing their dispersion between the tubes.

Although our study represents a first step towards understanding the decision-making process in trail-laying ants in a different context than foraging, we are aware that the experimental conditions we tested are far from the natural situations of nest relocations in the wild. One should ask especially what would be the influence of the queen during the migration process. Once she has migrated to a site, her attraction of workers (Coglitore and Cammaerts 1981) should strengthen the aggregation

feedback induced by workers already clustered. Thus, the queen should favor the emergence of a clear-cut choice in reinforcing the symmetry-breaking, thus preventing the splitting of the colony under migration. One major difference between the selection of an aggregation place, as studied here, and that of a nest site is the temporal and spatial scale over which the phenomenon takes place. Considering its dynamic, the selection of an aggregation site in *M. barbarus* closely resembles the exploitation of food sources in ant species using mass communication, with the remarkable difference of the "social" resting time modulation. It takes only a few minutes for a group of ants to initiate a migration and select an aggregation site while it takes several hours or days for a colony to choose a nest site.

In social insects, collective movements are not restricted to foraging or house-hunting but also contribute to the organization of the nest, which might be seen as a network of clusters. During their life-cycle, insects frequently change the place of various items such as brood or food, and also distribute themselves between chambers depending on the local variations of humidity and temperature (Seeley and Heinrich 1981; Hölldobler and Wilson 1990; for *M. barbarus* Cerdan 1989). Bearing in mind the difference between the spatial and temporal scales of both phenomena, the nest organization and nest migration might both benefit from recruitment and aggregation mechanisms. The formation of bivouacs in army ants is one of the most impressive examples where the combination of both mechanisms reaches its highest degree (Schneirla 1971; Gotwald 1995).

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