Noise improves collective decision-making by ants in dynamic environments

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Recruitment via pheromone trails by ants is arguably one of the best-studied examples of self-organization in animal societies. Yet it is still unclear if and how trail recruitment allows a colony to adapt to changes in its foraging environment. We study foraging decisions by colonies of the ant *Pheidole megacephala* under dynamic conditions. Our experiments show that *P. megacephala*, unlike many other mass recruiting species, can make a collective decision for the better of two food sources even when the environment changes dynamically. We developed a stochastic differential equation model that explains our data qualitatively and quantitatively. Analysing this model reveals that both deterministic and stochastic effects (noise) work together to allow colonies to efficiently track changes in the environment. Our study thus suggests that a certain level of noise is not a disturbance in self-organized decision-making but rather serves an important functional role.

Keywords: decentralized decision-making; mass recruitment; *Pheidole megacephala*; pheromone trails

1. INTRODUCTION

Groups of animals often make decisions collectively without any central control or coordination (Camazine *et al.* 2001; Couzin *et al.* 2005). Probably, the best-studied animal groups are the social insects where colony-level decisions emerge from simple interactions between myriads of individuals that only process local information (Camazine *et al.* 2001; Detrain & Deneubourg 2006, 2008). For example, both ants and bees are capable of selecting the best nest site out of several alternatives during emigration and reproductive swarming (Mallon *et al.* 2001; Seeley & Buhrman 2001). Honeybee (*Apis mellifera*) colonies are able to allocate most of their foragers to the best possible food patches while largely ignoring patches of inferior quality (Seeley 1995). Likewise, ant colonies form trails to food sources that follow the shortest path (Goss *et al.* 1989; Beckers *et al.* 1992; Vittori *et al.* 2006) and more generally maximize foraging time (Dussutour *et al.* 2006). Such ant trails are formed using pheromones, chemicals that the ants leave behind when returning to the nest from a profitable food source in order to mark the path leading to the food (Hölldobler & Wilson 1990). These pheromones recruit other nestmates to foraging activities and guide them to the discovered food. Newly recruited foragers in turn reinforce the trail with their own pheromone, thus increasing the probability that other ants will also use and reinforce it.

Many ant species have to compete for ephemeral food sources that constantly change location (Pharaoh's ants, Beekman *et al.* 2001; Argentine ants, Human & Gordon 1996), and their capacity to do so is highly dependent on their ability to adapt the colony's foraging patterns to changes in the environment. A particularly interesting question is how a colony modifies an already established foraging pattern when a new (and potentially better) food source is discovered.

Interestingly, the conventional wisdom derived from controlled laboratory experiments is that many mass-recruiting ant species are not able to efficiently exploit the discovery of a better food source once the colony is already exploiting one (Beckers *et al.* 1990; Traniello & Robson 1995) and this is in agreement with the predictions of existing mathematical models (Nicolis & Deneubourg 1999; Camazine *et al.* 2001). For example, in *Lasius niger*, ants generally do not modify their foraging path once it has been established even when a shortcut to a food source is introduced (Beckers *et al.* 1990).

Here we study the ability of the big-headed ant *Pheidole megacephala* to adapt to dynamically changing foraging conditions. *Pheidole megacephala* uses mass recruitment to exploit food sources. We describe experiments that demonstrate that *P. megacephala* is able to quickly adapt its foraging behaviour when food sources appear or disappear. We then introduce continuous stochastic models based on Itô calculus (Gardiner 2004) and Fokker–Planck equations (Risken 1989) and apply these to our experiments. We construct a quantitative mathematical model that explains our experimental results. Our model suggests that two factors contribute to the ants' ability to adapt: randomness in the decision-making process (noise) and deterministic components of the ants'

behaviour. Our mathematical analysis is supported by individual-based simulations that confirm our experimental findings and validate the formal model.

2. MATERIAL AND METHODS
(a) *Rearing conditions*
We collected 21 colonies of 2000–3000 workers and four to six queens in Sydney, Australia. Ants were installed in eight tube nests (10 cm length, 1.5 cm in diameter) covered with black paper. These tubes were placed in a rearing box (30*20*15 cm) with walls coated with Fluon to prevent ants from escaping. Colonies were kept at room temperature ($25 \pm 1°C$) with a $12:12$ L:D photoperiod. We supplied each colony with water and a mixed diet of vitamin-enriched food (Bhatkar & Whitcomb 1970) supplemented with mealworms.

(b) *Experimental set-up*
In each experiment, a colony was starved for 5 days before given access to two food sources placed on two platforms (70×70 mm) at the end of a Y-shaped bridge. The two branches of the Y-shaped bridge differed in length with one branch measuring 180 mm in length ('long') and the second 60 mm ('short') (figure 1a). Food consisted of 3 ml of 1 M sucrose solution contained in a small cavity carved in a block of paraffin wax. The whole experimental set-up was isolated from any sources of disturbance by surrounding it with white paper walls.

Two versions of the experiment were conducted using either a static or a dynamic environment. In the dynamic version, the ants had access to the food sources via the two branches for one hour (first phase). After 1 h, the short branch was blocked at its end (figure 1b), preventing ants from reaching the food source for one hour (second phase). After 2 h, the short branch was re-opened allowing ants to reach the food source again (figure 1c, third phase). In the static version, the experimental conditions remained unchanged and the ants had access to both food sources for 3 h. For each environment, we replicated the experiment 21 times using each colony once. All trials were filmed using a video camera placed over the bridge.

(c) *Data collection*
To assess traffic flow at the collective (colony) level, we measured traffic on both bridges every minute for the duration of the trials. We measured the flow of outbound ants at a point 1 cm from the junction onto each branch. Counting began as soon as the first ant discovered the bridge and climbed onto it. We used a two-way ANOVA with repeated measures on time to test for the effects of environment (static or dynamic) and time interval on the flow of workers. To test whether ants preferred one branch over the other (asymmetric distribution), or whether they showed no preference (symmetric distribution), we used a binomial test on the number of ants travelling on each branch for each replicate. The null hypothesis was that ants choose both branches with equal probability (Siegel & Castellan 1988). We assumed that a branch was selected when the binomial test showed a significantly higher number of foragers on one branch.

3. RESULTS
(a) *Experimental results*
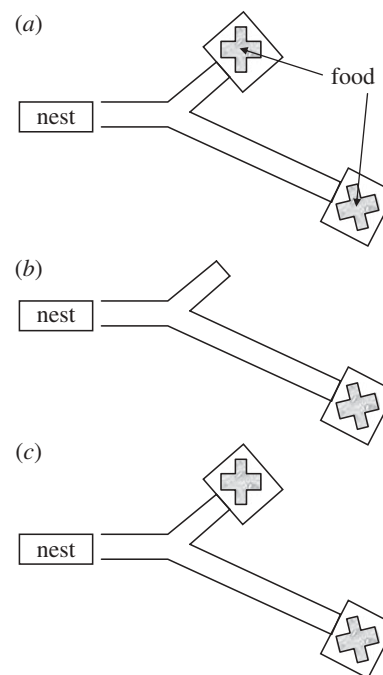Total traffic volume and recruitment were comparable in the dynamic and the static environment (figure 2,

Figure 1. Experimental set-up for dynamic environment. (*a*) First phase: 0–60 min, (*b*) second phase: 60–120 min and (*c*) third phase: 120–180 min.

two-way ANOVA with repeated measures on time interval: environment effect, $F_{1,40} = 0.45$, $p = 0.236$, interaction environment × time effect, $F_{179,40} = 1.41$, $p = 0.182$). The flow reached a peak after about 40 min in both environments (time effect: $F_{179,40} = 64.10$, $p < 0.001$). The similarity in recruitment dynamics suggests that the trail-laying frequency (i.e. the number of ants that deposit pheromone) did not depend on the experimental set-up.

Both traffic volume and recruitment dynamics on each branch were influenced by the environment (figure 2, two-way ANOVA with repeated measures on time interval: environment effect, $F_{1,40} = 26.80$, $p < 0.001$ and $F_{1,40} = 8.45$, $p < 0.001$; interaction environment × time effect $F_{179,40} = 29.05$, $p < 0.001$ and $F_{179,40} = 14.98$, $p < 0.001$ for the long and short branches, respectively). In the dynamic environment, traffic on the long branch significantly increased after the short branch was blocked and decreased when it was re-opened (time effect: $F_{179,40} = 37.121$, $p < 0.001$). Conversely, flow on the short branch significantly decreased after the short branch was blocked and increased when it was re-opened (time effect: $F_{179,40} = 57.18$, $p < 0.001$). In the static environment, the traffic on both branches stayed relatively constant and followed a typical trail recruitment process (Pasteels & Deneubourg 1987).

In the static experiment, most ants travelled on the short branch in 18 out of the 21 replicates after 3 h (figure 3b, binomial test: $p < 0.05$). In the dynamic version, most ants travelled on the short branch during the first phase in all 21 replicates (figure 3a, binomial test: $p < 0.05$). During the second phase, when the short branch was blocked, in 18 out of the 21 replicates ants refocused their traffic on the long branch (figure 3a, binomial test: $p < 0.05$). Only in one replicate did the ants still prefer the short branch even though food was no longer
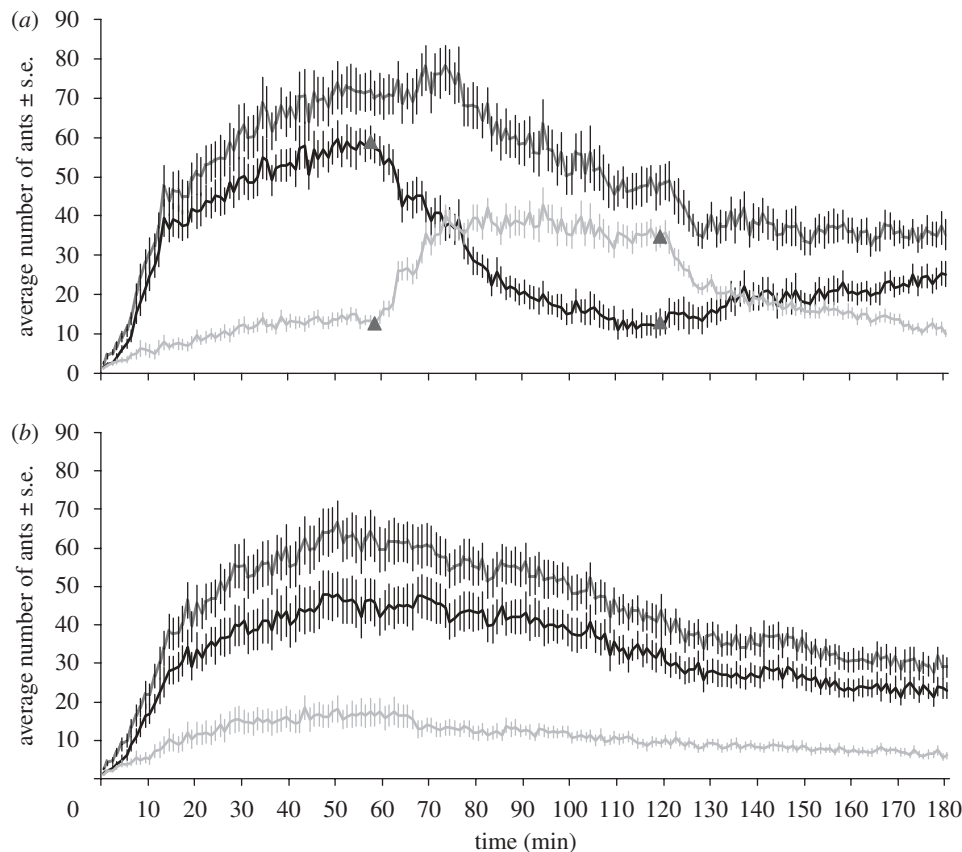
Figure 2. Average number of outbound ants per minute crossing the two branches of the bridge over time in (*a*) dynamic and (*b*) static environment. $n = 21$ replicates for each environment. Filled triangle indicates when the short branch was blocked and when it was re-opened. Black line, short branch; light grey line, long branch; dark grey line, total flow.

present. In two replicates, the ants did not choose either of the branches (i.e. they used both branches equally). Finally, when the short branch was re-opened, in nine out of the 21 replicates ants showed a significant preference for the short branch after one hour (figure 3*a*, binomial test: $p < 0.05$). In six out of the 21 replicates, most ants continued to travel on the long branch (binomial test: $p < 0.05$). In six out of the 21 replicates, both branches were used equally (binomial test: $p > 0.05$). However, if we considered the last 30 min of the experiment, in 16 out of the 21 replicates ants chose the short branch (binomial test: $p < 0.05$).

(b) *Standard model of mass recruitment*
The most widely used class of mathematical models for foraging in mass-recruiting ant species in static environments is based on systems of ordinary differential equations (Deneubourg *et al.* 1990; Nicolis & Deneubourg 1999). Let the amount of pheromone on the two branches be denoted by c_i. The probability of an individual ant to choose either branch is

$$p_i = \frac{(k + c_i)^\alpha}{\sum_{j=1,2} (k + c_j)^\alpha}, \qquad (3.1)$$

where k and α are constants fitted to experimental data. Each individual forager deposits an amount of pheromone q_i upon its return to the nest. The total number of foragers leaving the nest per time unit typically depends on the amount of trail pheromone present among other factors. Assuming a total flow of Φ foragers, the number

of foragers on branch i is $p_i \Phi$ and the build-up of the pheromone levels on each branch is

$$\frac{dc_i}{dt} = p_i q_i \Phi - \rho c_i, \qquad (3.2)$$

where ρ is the rate constant for pheromone evaporation (Dussutour *et al.* 2009).

Let branch 2 be the superior path, for example, because it is shorter or leads to a food source of higher quality. There are two reasons why branch 2 may attract more traffic than branch 1. When it is shorter, it receives pheromone deposits by returning foragers earlier thus getting a head start in the competition or ants may modulate their pheromone deposit depending on the quality of the food source. While some species modulate the amount of pheromone deposit explicitly with food or path quality, other factors, such as home range marking (Devigne & Detrain 2006) or higher rate of U-turns on longer branches (Camazine *et al.* 2001), can also lead to indirect deposit modulation. As we are only interested in the fixpoints of the model, we can summarize the implicit or explicit deposit modulation in all of these cases by assuming $q_1 < q_2$.

The expected steady-state behaviour of the system is predicted by its fixpoints. It is well known that this model exhibits either one or three fixpoints (Nicolis & Deneubourg 1999; Camazine *et al.* 2001). The first fixpoint corresponds to a proportional usage of branches (i.e. pheromone on both paths and in the case of equal deposits $q_1 = q_2$ both sources are exploited equally). The other two fixpoints correspond to the situation
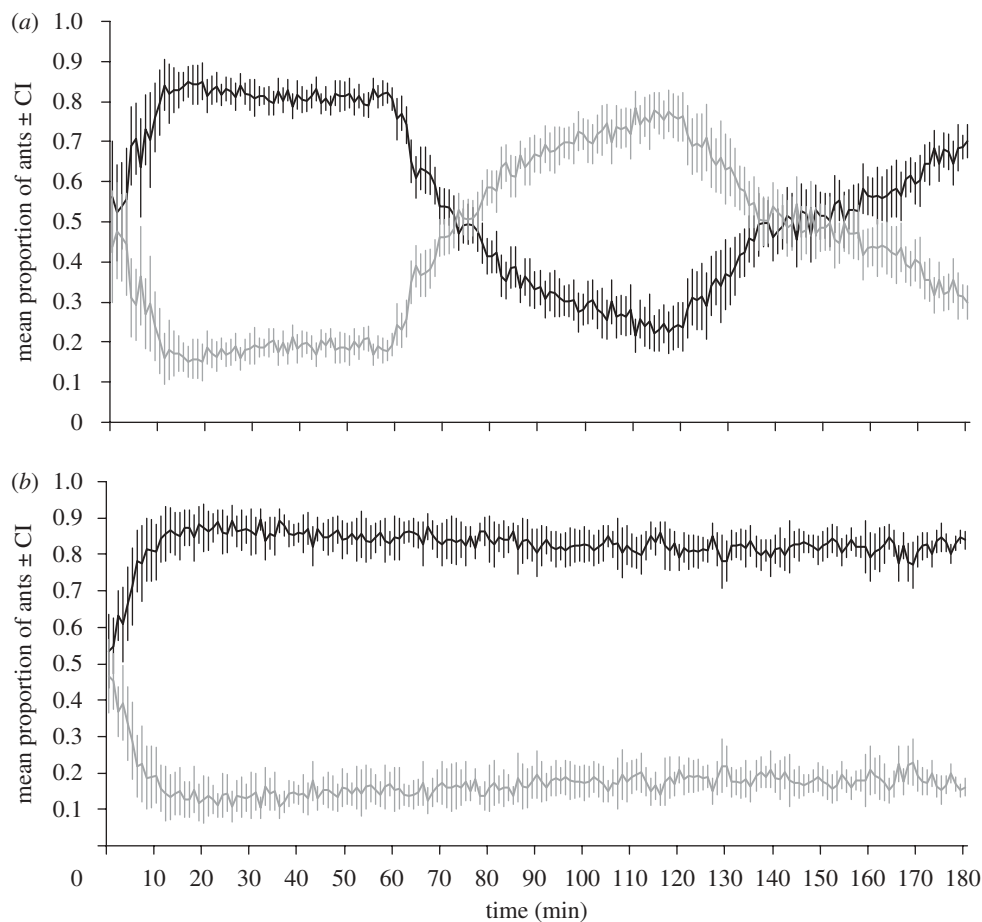
Figure 3. Mean proportion of outbound ants per minute crossing the two branches of the bridge over time in (*a*) dynamic and (*b*) static environment. $n = 21$ replicates for each environment. Black line, short branch; grey line, long branch.

where predominantly one branch is exploited. The exact proportion of exploitation depends on the parameters k, α, Φ and ρ and the proportion q_1/q_2. The fixpoints are only stable in limited parameter ranges. For $k = 0$, $\alpha < 1$, only the first fixpoint $p_1^* = (1 + (q_2/q_1)^{\alpha/(1-\alpha)})^{-1}$ is stable, but it exchanges its stability with the other two fixpoints $p_1^* = 0$ and $p_1^* = 1$ at $\alpha = 1$. For $\alpha > 1$, the other two fixpoints are stable: the one that corresponds to exclusive exploitation of the superior branch as well as the one that corresponds to only exploiting the inferior branch. The model has experimentally been fitted to the behaviour of real ant colonies, specifically for *L. niger* with $\alpha = 2$ and $k = 6$ (Beckers *et al.* 1993; Camazine *et al.* 2001).

For $k > 0$, the situation remains in principle unchanged, but there will always be a residual amount of exploitation of the less used branch. This amount depends on k. In the case of identical deposits and $\alpha = 2$, the first fixpoint (equals exploitation) is stable only for $(q\Phi/2\rho k) < 1$.

Note that the analysis so far does not predict which of the two stable fixpoints will be observed in any given experiment. This depends on the differences between food source qualities and path lengths and on the times at which the two sources are first discovered. However, when the differences (and thus deposit ratio q_2/q_1) and the flow Φ are large enough, the superior branch will generally be exploited most (Camazine *et al.* 2001). Once a stable fixpoint has been reached, the

ants' behaviour is locked-in regardless of changes in the reward ratio. A model with these two stable fixpoints is thus in agreement with the observation that a colony will not adapt if the better branch is presented with significant delay.

To apply this model to a dynamic foraging environment, we need to consider each phase of the experiment separately and use the final state of each phase as the starting state of the subsequent phase. If the food sources change or become unavailable, the reward q_1 must be adjusted accordingly for the next phase. The switch from phase 2 to phase 3 in our experiments is thus essentially equivalent to presenting the shorter branch with significant delay. With two stable fixpoints, the model therefore cannot correctly predict the third phase of our experiments, where we see a switch back to the shorter branch after the colony had established a trail onto the longer branch.

(c) Extended stochastic model
To understand what causes the switch back to the short branch, we need to analyse which factors influence the stability of the second fixpoint ($c_2 < c_1$, corresponding to most pheromone on the longer/inferior path). One factor that is known to have such an effect is the total flow of foragers. We thus have to take the experimentally observed decrease in total flow into account. We will not attempt to model the dependence of the flow on other

factors explicitly, but instead match a time-dependent flow function $\phi(t)$ to the experimental data (figure 2). We approximate an upper bound on the flow reduction by a linear reduction from 100 to 50 per cent from $t = 60$ to 120 min

$$\phi(t) = \begin{cases} 1 & t < 60 \\ 0.5 + (120-t)/120 & \text{for} \quad 60 \leq t \leq 120 \\ 0.5 & t > 120 \end{cases} \quad (3.3)$$

Another factor that can influence the stability of the fixpoints is random fluctuations (noise) in the decision-making process. Such noise can be caused, for example, by differences in trail following behaviour between individuals, by individuals that vary their behaviour over time or in response to environmental fluctuations. Our experiments showed large fluctuations in ant traffic on each branch, thus suggesting that such noise is indeed prevalent. We approximate noise by integrating into the standard model a constant level σ of additive Gaussian white noise. By replacing equation (3.2) in the previous model with its stochastic equivalent, we obtain a two-dimensional system of Îto stochastic differential equations as the extension of the deterministic model

$$\frac{dc_i}{dt} = p_i q_i \phi(t) - \rho c_i + \sigma \frac{dW_i}{dt} \quad (i = 1, 2). \quad (3.4)$$

Such equations, in which W_i denotes a Wiener process (white noise), define a diffusion in the phase space of the underlying probability distribution. To simplify the technical discussion, we rewrite the two-dimensional model into a single dimension (for details, see electronic supplementary material, appendix A). With $\alpha = 2$, as fitted to experiments, we arrive at

$$dc_1 = \mu(c_1)dt + \sigma dW \quad (3.5)$$

with

$$\mu(x) = q_1 \phi(t) \frac{(k+x)^2}{(k+x)^2 + (k + ((Q_1 Q_2/\rho) - Q_2 x)/Q_1)^2} - \rho x, \quad (3.6)$$

where c_1 is the level of pheromone on the longer (inferior) branch and $Q_i = \Phi q_i$. We have derived the parameters for this model by performing a parametric grid search for the least squares match with the data given in figures 2 and 3. This yields: $k = 12$, $q_1 = 0.09$, $q_2 = 0.13$ and $\rho = 0.00085$.

We plot dc_1/dt at $t = 120$ for these parameters but without noise ($\sigma = 0$) in figure 4a.

Clearly, c_1 will eventually converge on one of the axis' intersections. The first and last axis intersection corresponds to stable fixpoints (exclusive use of a single source), whereas the middle point is unstable. As is shown in figure 4a, the flow reduction at $t = 120$ to 50 per cent of the initial flow reduces the stability of the highest fixpoint but does not completely destabilize it.

We also observed frequent U-turns in the experiments. If a large number of ants turn from the long branch to the short branch without returning to the nest first, then this could speed up or even trigger the switch back to the short branch. Again we do not attempt to model the number of U-turns as a dependent variable, but instead

view it as a time-dependent parameter $u(t)$ which we derive from the experimental data. We chose $u(t)$ so as to approximate the maximum number of U-turns that could affect the switch from the long to the short branch (e.g. only U-turns directly from the long branch onto the short branch are included; this value is derived from experimental observations (A. Dussutour 2007, personal observation). We integrate U-turns into the model by modifying the effective probabilities to take either branch

$$u(t) = \begin{cases} 0 \\ 0.07 \end{cases} \text{for} \quad \begin{matrix} t < 120 \\ t \geq 120 \end{matrix}, \quad (3.7)$$

$$\breve{p}_1(t) = (1 - u(t))\, p_1(t)$$
$$\breve{p}_2(t) = 1 - \breve{p}_1(t) \quad (3.8)$$

and

$$\frac{dc_i}{dt} = \breve{p}_i q_i \phi(t) - \rho c_i + \sigma \frac{dW_i}{dt}. \quad (3.9)$$

The effect of adding U-turns is indeed that the second fixpoint is destroyed and that the colony ultimately switches back to the shorter branch. This is evident from figure 4b, which shows the predicted probability to choose the shorter branch taking U-turns and flow reduction into account. However, the time needed to execute the switch is exceedingly high: for the U-turn rates observed in the experiment, the model predicts that it will take more than 250 min until both branches are used equally ($p_1 = 0.5$). This is clearly not consistent with our experimental outcome. Because we only included U-turns that could facilitate a switch (ants turning from the long branch onto the short branch) the actual time to switch would even be longer than in our estimate if U-turns were the only mechanism.

If we include noise, our model predictions nicely fit our experimental observations (figure 4c). Random fluctuations can significantly change the behaviour of the model because any fluctuation that pushes the pheromone level on the longer branch momentarily to the left of the second axis intersection of dc_1/dt in figure 4a will be amplified and ultimately lead to a switch to the short branch. The time development of the complete stochastic model taking noise, flow reduction and U-turns into account matches the experimental data almost precisely (figure 4c). It is also worth noting that there is no appreciable difference between the predictions of the model that includes (solid line) and excludes U-turns (dotted line). This is not really surprising as a U-turn that is 'uninformed' and not triggered by some explicit information on the inferiority of the currently used branch could also be interpreted as a form of noise.

The expected time $t(x)$ for the colony to switch back to the shorter branch in phase 3 is given by the first passage time for the model in equations (3.5) and (3.6) (for details, see electronic supplementary material, appendix A)

$$t(x) = \int_a^x \left(\frac{2}{\psi(y)} \int_y^b \frac{\psi(z)}{\sigma^2(z)} dz \right) d$$

$$\text{with} \quad \psi(x) = e^{\int_a^x (2\mu(y)/\sigma^2(y))dy}.$$

We plot the first passage time against the noise level in figure 4d. It confirms that a higher level of noise allows
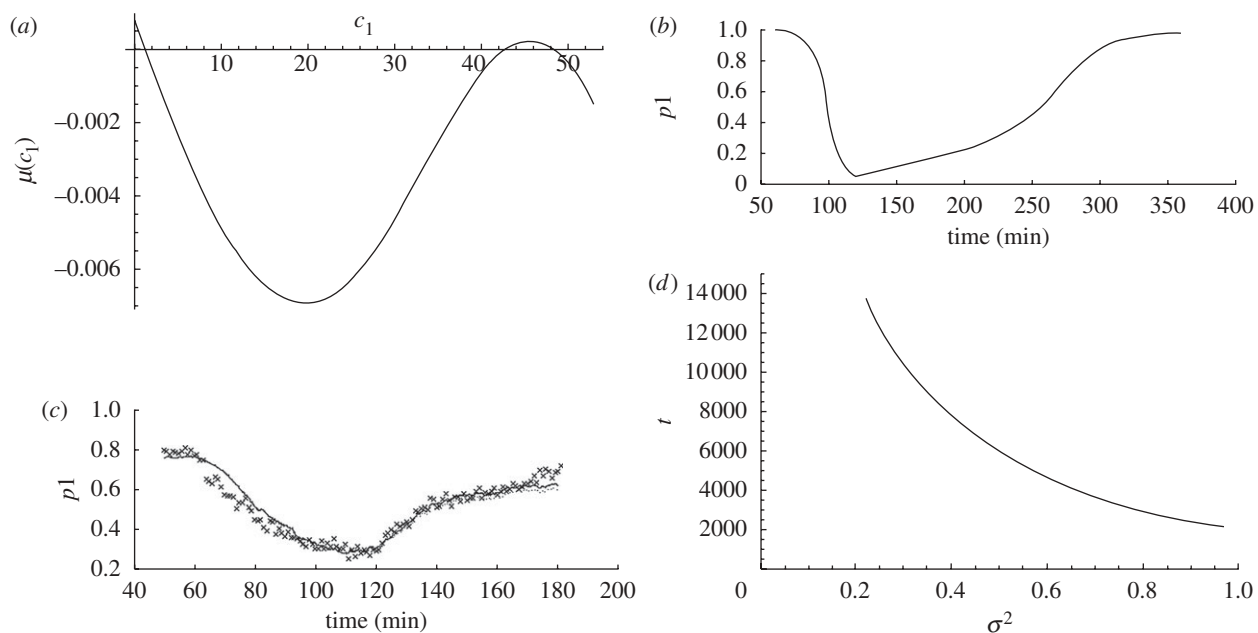
Figure 4. (*a*) Predicted derivative of pheromone level on the longer branch after the shorter branch is reopened. (*b*) Predicted probability to choose the shorter branch taking U-turns and flow reduction but no noise into account ($\sigma = 0$). (*c*) Predicted probability to choose the shorter branch taking noise ($\sigma = 1$), U-turns and flow reduction into account (solid line, including U-turns; dotted line, excluding U-turns; crosses, experimental data). (*d*) Predicted first passage time (expected time until the long branch is no longer used after the short branch became available again in phase 3).

a significantly faster switching. Our stochastic model thus also accounts for the classical experiments like those for *L. niger* in which much lower noise levels have been observed (figure 5, Dussutour *et al.* 2005). At such low noise levels, the first passage time is well beyond the duration of the experiment. We thus expect to see such a switch only in very rare cases. Note that the stochastic nature of the model also accounts for the fact that there is a small fraction of trials in which *P. megacephala* did not switch back to the better source.

4. DISCUSSION

Big-headed ants were able to adjust their recruitment as a function of environmental change. At each stage, most colonies were able to choose the best foraging opportunity. In the first stage, the short branch was selected most often. When the food source at the end of the short branch was removed, the colonies were able to quickly redirect their foraging activity to the long branch. Finally, when the food source was reconnected to the short branch, the ants preferentially exploited this food source in most trials.

Our modelling reflects known foraging strategies of both *P. megacephala* and *L. niger*. *Lasius niger* tends aphid colonies which are more or less permanent food sources (e.g Flatt & Weisser 2000). This is in contrast to *P. megacephala* which is an invasive species that exploits ephemeral food sources (Dejean *et al.* 2005, 2007). In addition to the already known causes for the ecological dominance of *P. megacephala* in areas where it has been introduced including its intrinsic ability to achieve unicoloniality, the absence or rarity of enemies (Hoffmann *et al.* 1999; Holway *et al.* 2002; Wilson 2003), our study suggests that the ability of this species to react to changes

in the environment may contribute to its dominance when introduced into new areas.

A simple deterministic standard model of mass recruitment that includes strong nonlinear trail feedback is highly sensitive to small differences in trail strength and fails to fully explain our experimental results. If the flow of ants is sufficient, the new trail on the short branch will never succeed in overcoming the continuing recruitment on the long branch. As our analysis has shown, a deterministic model can only explain our experimental results if the nonlinear feedback is moderated through, for example, flow reduction or U-turns. We have also shown that noise affects the speed with which such switches occur. In a deterministic model that predicts switching, c_1/c_2 can only have a single stable fixpoint. This typically means a proportional exploitation of both food sources. It is important to realize that noise can even make the switch possible if the underlying deterministic model has two fixpoints (and thus does not exhibit switching). For this reason, taking noise into account allows us to explain switching even in models that describe a unanimous collective decision for one of two choices if both choices have the same utility (rather than a proportionate exploitation of both sources). Noise can thus play a beneficial role by facilitating quick transitions to more advantageous foraging behaviours, regardless of whether this transition can in principle be explained through deterministic effects. Similar advantages of noisy decision-making for the efficient exploitation of food sources have previously been explored in (Nicolis *et al.* 2003) for the simpler case of static environments.

It is possible that additional deterministic influences are at work in our experiments which our current model does not capture. Specifically, recent work (Dussutour *et al.* 2009) suggests the presence of a second pheromone
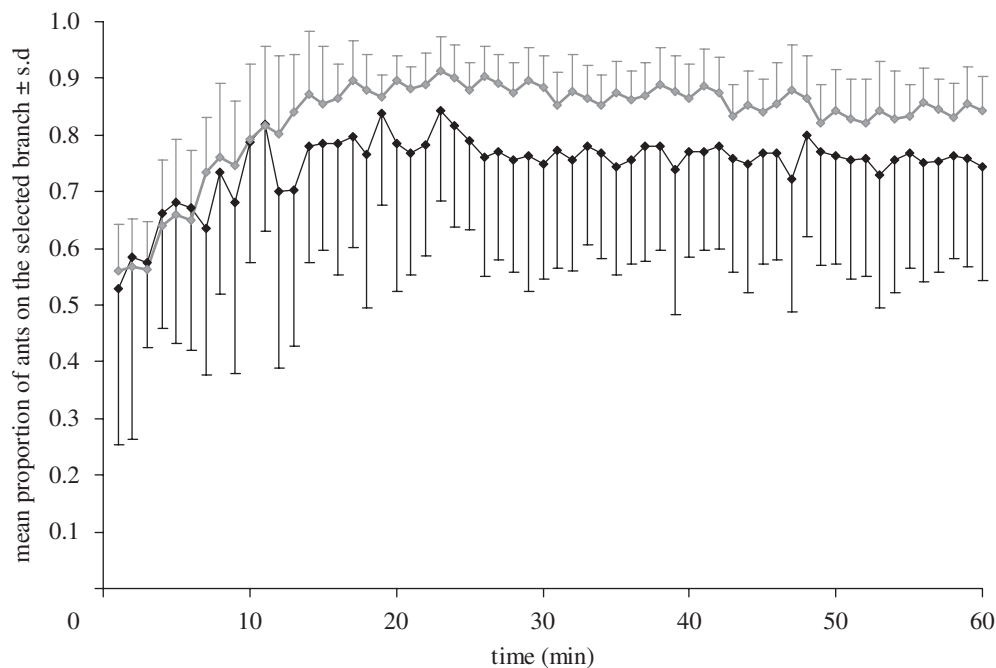
Figure 5. Comparison of variance between *P. megacephala* (black line) and *L. niger* (grey line): proportion of ants on the selected branch when ants are given a choice between two branches of equal length (60 mm). $n = 15$ replicates for each species.

in *P. megacephala* which is hypothesized to allow colonies to track changing foraging conditions more efficiently than with a single pheromone. However, these experiments used a symmetrical foraging set-up with identical food sources and thus did not investigate the choice between two alternatives that differed in quality.

Even though stochastic versions of the standard model have been studied before, we are only aware of one other analytical study (Nicolis 2004). Contrary to our study, Nicolis (2004) analysed the influence of noise on the choice between two equal food sources in a static environment. Non-analytical versions of the standard model have used Monte Carlo simulations to investigate dynamic scenarios. One such study also showed that noise can play a functional role in switching between food sources (Nicolis & Dussutour 2008). The study of Nicolis & Dussutour (2008) differs from ours in that it did not verify the model with experimental data nor did it include an investigation of the type of switch we see in phase 3 of our experiments, i.e. the switch to a better food source after the colony has already established a steady-state foraging pattern for another source.

Generally, Monte Carlo simulations of the standard model only show the effect of intrinsic noise that originates from the fact that each ant performs its path choice as a Bernoulli trial. Our analytic diffusion model takes additional fluctuations into account that are not intrinsic to this choice mechanism. What could be the biological origins of such fluctuations? One well-known source of noise is related to the ability of foragers to faithfully follow a chemical trail. Recruits may lose the trail and may make 'wrong' choices at junctions of the trail. It has been discussed in earlier work (Deneubourg *et al.* 1983) that the function of such 'lost' foragers may be to (re)-discover a better food source or a shorter path. Hence, under dynamic conditions, there is an optimal error level that minimizes the time needed for discovering

better food sources and which maximizes foraging efficiency. However, it is important to realize that noise is a more general phenomenon than ants losing the trail and may be induced by a large variety of sources. Generally, the behaviour of individuals never conforms exactly to the statistical average. Rather it exhibits variations, both between individuals and for each individual over time. For example, the amount of pheromone deposit per trip may vary and individual resting times and recruitment thresholds may differ (Mailleux *et al.* 2000, 2003, 2005). Unlike 'lost foragers', such fluctuations do not directly favour the (re)discovery of alternative sources. Instead, they simply introduce a small amount of variability (noise) into the decision-making. Such undirected noise, as a general systemic feature, can be sufficient to enable the system to behave adaptively.

(a) General implications for self-organizing systems

The analysis of our model shows that we gain the most complete understanding of collective decision-making in mass-recruiting ants if we interpret it as stochastic attractor switching. The same should hold true for other related types of social decision-making, such as market trends (Weisbuch & Stauffer 2000) or the way innovations are adopted (Capasso & Bakstein 2005).

Such noise-induced switching between two system states can in fact be understood as an instance of aperiodic stochastic resonance (Gammaitoni *et al.* 1998), a phenomenon that is widely observed in natural systems. Specifically, it enables sensory systems to track subthreshold signals (Moss *et al.* 2004). It also has direct technical applications, for example, for efficient encoding of auditory information in cochlear implants (Morse & Evans 1996). To the best of our knowledge, our analysis is the first account of aperiodic stochastic resonance in a macroscopic self-organized system.

Our results are not only interesting in the context of natural systems but may have far-reaching implications for applications of self-organization in engineering artefacts. They are specifically relevant to swarm intelligence (Bonabeau *et al.* 1999), i.e. to the design of self-organized optimization algorithms based on the mechanisms of collective behaviour in biological groups, such as ant colony optimization algorithms (Dorigo & Stützle 2004). Our results indicate that noise should be taken into account as a constructive component when engineering such systems: it may be advantageous to use controlled injection of noise into such systems to enable them to track changes in the environment efficiently.

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