

# Noise-induced Adaptive Decision-Making in Ant-Foraging

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**Abstract.** Ant foraging is a paradigmatic example of self-organized behavior. We give new experimental evidence for previously unobserved short-term adaptiveness in ant foraging and show that current mathematical foraging models cannot predict this behavior. As a true extension, we develop Itô diffusion models that explain the newly discovered behavior qualitatively and quantitatively. The theoretical analysis is supported by individual-based simulations. Our work shows that randomness is a key factor in allowing self-organizing systems to be adaptive. Implications for technical applications of Swarm Intelligence are discussed.

## 1 Introduction

Groups of humans or animals often make decisions collectively without any central control or coordination. The paradigmatic example of self-organized groups are colonies of social insects, such as ants and bees, whose strikingly organized and seemingly purposeful behavior at the group level is organized without any central “master plan” [4]. Their complex behavior at the colony level emerges from simple interactions between myriads of individuals that only process local information [19]. Such decentralized coordination exhibits a number of properties that are highly desirable in technical applications, specifically robustness, adaptiveness and parallelism. Hence, social insect behavior has been used as an inspiration for a wide range of engineering tasks [2, 13].

Despite the central importance of self-organized decision-making for many natural and technical systems, the theoretical understanding of its fundamental properties is still in its infancy. A core problem is that there is very little insight into how self-organized processes work in dynamic environments. Most research addresses only static conditions. Yet, being able to *adapt in dynamic environments* on all timescales is crucial for almost all natural systems and for many engineering artifacts using similar organizational principles.

Foraging in mass-recruiting ant species is arguably the best understood form of self-organized behavior, and detailed knowledge about different forms of organization as well as quantitative and qualitative mathematical models are available [4]. However, until recently this research has focused almost entirely on static environments where the available resources are constant. The conventional wisdom is that the ability of ants to quickly adapt to a changing environment is

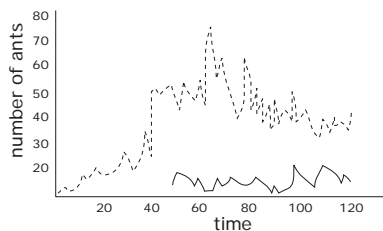
generally very limited, and this is in agreement with the predictions of existing mathematical models. Recently new experiments with dynamic environments have started to cast some doubt on the scope of these models. These new experiments clearly demonstrate that at least some mass recruiting ant species can flexibly and quickly adapt their foraging behavior to environmental changes. As the standard models cannot explain this adaptive decision-making, a more powerful way of modelling is required. The purpose of the present paper is to introduce such a type of model.

We will show that the conventional models have limited predictive power because they are mean field descriptions based on the general assumption that the net influence of noise is zero. As we will show, this is not the case in dynamic environments. Here, noisy communication has a crucial role in allowing ant colonies to behave adaptively. Our technical contributions are three-fold: Firstly, we give new experimental evidence for short-term adaptation in the foraging behavior of the mass recruiting ant species *Pheidole megacephala*. Secondly, we introduce continuous stochastic models based on Itô diffusions [12] and Fokker-Planck equations [18] as a new tool for theoretical research in ant behavior. Thirdly, we apply this method to our experiments obtaining a quantitative mathematical model that explains the adaptation and coincides with the conventional model in the noise-free limit. Our mathematical analysis is supported by individual-based simulations which confirm our experimental findings and validate the formal model.

## 2 Standard Models of Ant Foraging

Mass recruiting ant species, such as *Lasius niger* and *Pheidole megacephala*, coordinate their foraging activities mainly using pheromone communication [14]. When returning from a food source to the nest, the foragers deposit pheromones on the paths they use. New foragers that venture out from the nest in search of food probabilistically follow the pheromone gradients in the environment and pheromone gradually evaporates over time. In this way a self-limiting positive feedback loop is created and increasingly more pheromone is deposited on the paths to food sources. As the amount of pheromone deposit is generally (directly) modulated by food source quality or (indirectly) by the distance of the food source to the nest, the majority of the traffic tends to converge on the paths to more desirable food sources [4].

A classical binary decision experiment to investigate this behavior is the “Y-Bridge” [4]. In this experiment the colony is presented with two food sources at the two ends of a forking path from the nest (Fig. 3, top). When the quality of



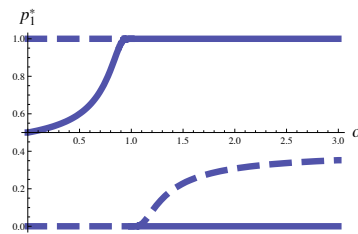
**Fig. 1.** Average Number of Foragers at Better Source [4]. Dashed: Both Sources Presented Simultaneously; Solid: Better Source Presented with Delay.

the food sources or the path lengths to the sources are different the ants typically make the correct collective choice: the vast majority of foragers converge on the shorter path or on the richer source, respectively. However, this is generally only true if both choices are present right from the beginning. If at first only the inferior choice is presented (longer path or worse quality) and the superior one is only added after the traffic has stabilized, the colony will generally *not* adaptively adjust and will stick with the inferior solution instead [4] (Fig. 1).

A widely used class of models that explains these and related experiments in *static environments* is based on dynamic systems using ordinary differential equations [8, 17]. Let the amount of pheromone on the two branches be denoted by  $c_1, c_2$ . In the standard model [8], the probabilities of an individual ant to choose either branch when leaving the nest are  $p_i = \frac{(k+c_i)^\alpha}{\sum_{j=1}^2 (k+c_j)^\alpha}$  where  $k, \alpha$  are non-negative constants fitted to experimental data. Each individual forager deposits an amount of pheromone  $q_i$  upon its return to the nest. While the total number of foragers leaving the nest per time unit in reality depends on the amount of trail pheromone present, it has been shown that this flux may be assumed to be constant without changing the characteristics of the model [17]. Assuming a constant total flux of  $\Phi$  foragers, the number of foragers on Branch  $i$  is  $n_i = p_i \Phi$ , and the development of the two pheromone levels is  $\frac{dc_i}{dt} = p_i Q_i - \rho c_i$  where  $\rho$  is the rate constant for pheromone evaporation,  $Q_i = \Phi q_i$ .

Let Branch 1 be the superior path. There are two reasons why it may attract more traffic than Branch 2: Either the food sources are of different quality and pheromone deposit is actively modulated by food quality ( $q_1 > q_2$ ) or Branch 1 is shorter and thus receives pheromone deposits by returning foragers earlier, i.e. it gets a head start in the competition. Pheromone deposit on the shorter path may also be (indirectly) modulated, for example due to a lower trail fidelity or a higher rate of U-turns on the longer branch [4] or due to home range marking [9].

It is well known that this model exhibits three fixpoints [4, 17]. The first fixpoint corresponds to a proportional usage of paths (i.e. pheromone on both paths and in the case of equal deposits  $q = q_1 = q_2$  both sources will be equally exploited). The other two fixpoints correspond to the situation where predominantly one source is exploited and the other resource is exploited far less, even for  $q_1 = q_2$ . The



**Fig. 2.** Standard Model Fixpoints.

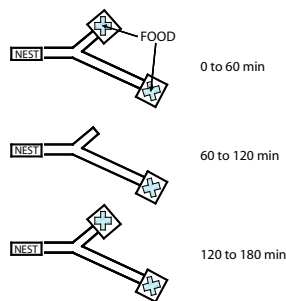
exact proportion of exploitation depends on the parameters  $k, \alpha, \Phi, \rho$  and the proportion  $q_1/q_2$ . The first fixpoint is only stable in a limited parameter range. The fixpoint diagram for  $p_1$  in Fig. 2 summarizes the situation for  $k = 0$  [15]. For  $\alpha < 1$  only the first fixpoint  $p_1^* = 1 / \left( 1 + \left( \frac{q_2}{q_1} \right)^{\frac{\alpha}{1-\alpha}} \right)$  is stable, but it exchanges its stability with the other two fixpoints at  $\alpha = 1$ . Interestingly, for  $\alpha > 1$  two fixpoints are stable: the one that corresponds to exclusive exploitation of the

superior source as well as the one that corresponds to only exploiting the inferior source. The model has experimentally been matched to the behavior of real ant colonies, specifically for *L. niger* with  $\alpha = 2, k = 6$  [4, 1]. When  $k \geq 0$  the situation remains in principle the same, but there will always be a residual amount of exploitation of the less used resource. This amount depends on  $k$ .

Note that the model so far does not fully predict which of the two stable fixpoints will be observed in any given experiment. The decision depends on the differences between food source qualities and path lengths and on the times at which the two sources are first discovered. However, it has been observed that the decision is successfully made for the superior choice in most cases if the differences (and thus deposit ratio  $q_1/q_2$ ) and the flux  $\Phi$  are large enough [4]. Once a stable fixpoint has been reached the behavior is locked regardless of changes in the reward ratio. It is thus in agreement with the model that the colony will not adapt if the better source is presented with significant delay.

### 3 Experiments with Dynamic Environments

To investigate the adaptiveness of foraging in the mass recruiting “big headed ant” *P. megacephala* we used a slightly modified version of the classical Y-bridge experiment. In each experiment, a colony starved for 5 days was given access to two equal food sources (3ml of 1M sucrose solution) placed on a platform (70 × 70mm) at the ends of a Y-shaped bridge with two branches of different length: 180mm



**Fig. 3.** Experimental Set-up

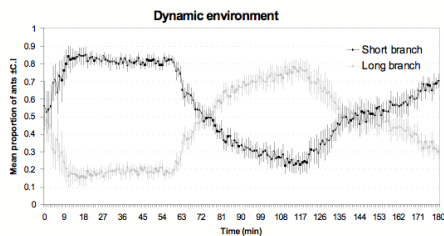
and 60mm (Fig. 3). The experiment had three phases. In the first phase (top) we let the colony forage freely for one hour at both sources. After this time the short branch was blocked at the level of the food source preventing ants from reaching this source in Phase 2 (middle). One hour later the short branch was reopened for Phase 3 (bottom). A control experiment was performed with 3 hours of duration in which no changes were applied to the set-up. We replicated the experiment with 21 colonies of approximately 2,000 workers each with brood and queen kept at room temperature ( $25 \pm 1^\circ C$ ) with a 12 : 12 L/D photoperiod. Fig. 4 shows the average proportion of the number of foragers on the branches. The behavior of *P. megacephala* is surprisingly different from that of *L. niger*: This species does indeed manage to adapt to the change in food sources (or their accessibility). It is obvious that the ants initially commit to the more desirable short branch and switch to the longer branch when the shorter one becomes unavailable in Phase 2. In Phase 3 the colonies generally switch back to the more desirable shorter branch.

We can attempt to model our experiment using the standard model and changing the deposit constants  $q_i$  when switching from one phase to another. There is nothing surprising about the switch from Phase 1 to Phase 2. As the

food source on the short branch becomes unavailable, this branch does not receive any further pheromone in Phase 2 and the pheromone left from Phase 1 simply evaporates until nothing is left. At the same time the longer branch still receives new recruitment pheromone. The ants therefore must eventually switch to the longer branch. The model predicts this. However, the switch from Phase 2 to Phase 3 is not as expected from the predictions of the standard model. At the end of Phase 2 sufficient time has elapsed for the colony to focus predominantly on the longer branch, and we know from control experiments that by this time the pheromone on the blocked shorter branch has evaporated sufficiently to not influence the path choice anymore. From Section 2 we can be certain the ants should not be able to refocus on the shorter branch when it is re-opened, because the traffic has reached a stable fixpoint.

It is crucial to realize that the standard model cannot be coaxed into any other behavior by tuning its parameters. Specifically, the only way to tune the model such that it switches the predominant exploitation from one resource to the other when the deposit ratio  $q_1/q_2$  changes after one branch has reached saturation is to set  $\alpha \leq 1$ .

However, for  $\alpha \leq 1$  the model has only one fixpoint and we should *always* observe this fixpoint in real experiments. What we do see, however, is that every trial has two possible outcomes. The standard model thus fails to predict Phase 3 correctly. The necessity to modify it is clear.



**Fig. 4.** Average Proportion of Foragers

## 4 Noise-induced Adaptiveness

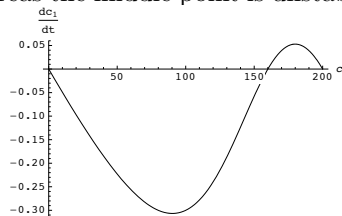
The question is, which crucial aspect of *P. megacephala*'s decision making does the standard model ignore. We will show that no new mechanism needs to be invoked. It is simply and somewhat counter-intuitively the noisiness of the decision making behavior which enables the colonies to behave adaptively. Despite the fact that the role of individual error in foraging has long been recognized [7, 16], current foraging models are generally mean-field descriptions, and errors are simply treated as average error rates. The fundamental problem with this is that mean-field models, strictly speaking, only give us a correct description if the behaviors of all individuals are identical (conforming to the average of their true behaviors). This simplification is not always justified. In the presence of non-linear responses, behavioral deviations of only a few individuals from the mean can trigger qualitative changes in the colony behavior. To model these fluctuations, we must use stochastic models. Leading researchers have called for analytic stochastic models of ant foraging in the past already [17]. This call is still echoed in the most recent surveys [13], but it has gone unanswered as yet. In this section we will derive a stochastic model of mass recruitment based on the standard model and show how it explains the newly observed effects.

We rewrite the two-dimensional model into a single dimension, exploiting  $p_1 = 1 - p_2$ . It is convenient to introduce a “re-normalized deposit”  $z = Q_2 c_1 + Q_1 c_2$  for which  $\frac{dz}{dt} = Q_1 Q_2 (p_1 + p_2) - \rho(Q_2 c_1 + Q_1 c_2) = Q_1 Q_2 - \rho z$ . Observe that  $z$  develops completely deterministically with finite limit  $\lim_{t \rightarrow \infty} z(t) = \frac{Q_1 Q_2}{\rho}$ . Note that  $z$  equilibrates quickly. We run each phase of the experiment long enough so that the pheromone levels are saturated. Thus, to describe the switching behavior between the phases we can replace  $z(t)$  with its limit and eliminate  $c_2$  from the model. From the standard model with  $\alpha = 2$  we obtain

$$\frac{dc_1}{dt} = Q_1 \frac{(k + c_1)^2}{(k + c_1)^2 + (k + \frac{Q_1 Q_2 - Q_2 c_1}{Q_1})^2} - \rho c_1 \quad (1)$$

$c_2$  is given implicitly by  $c_2(t) = \frac{z(t) - Q_2 c_1(t)}{Q_1}$ . We plot the general shape of  $\frac{dc_1}{dt}$  for the relevant parameter region in Fig. 5. Clearly  $c_1$  will eventually converge on one of the axis intersections. The first and last axis intersection correspond to stable fix points (exclusive use of a single source), whereas the middle point is unstable.

Let  $c_1$  stand for the pheromone level on the *longer* branch. The stability of the highest fixpoint of  $c_1$  in the mean field model (corresponding to most pheromone on the longer/inferior path and thus its almost exclusive use) is what makes it impossible for the model to switch to the exploitation of the superior food source when it is re-introduced at the commencement of



**Fig. 5.** Drift term.

Phase 3. However, if we take random fluctuations into account this is no longer true: Any fluctuation that pushes the pheromone level on the longer branch momentarily to the left of the second axis intersection will be amplified and lead to a switch to the short branch. As we observe reasonably large random fluctuations of the forager counts on each branch in experiments, the assumption of such random fluctuations is justified. The first reason why the counts must be “noisy” is that each ant makes an individual binary decision with decision probability  $p_i$  (Bernoulli trial). Thus the distribution of the number of foragers selecting path  $i$  is given by the binomial distribution  $B(N, p_i)$  with mean  $N \cdot p_i$  and variance  $\sigma^2 = N p_i (1 - p_i)$ . If we want to be able to model possible developments of individual trials (instead of just averages), we have to replace  $p_i$  with  $(p_i + \sigma W)$  where  $W$  is a (Gaussian) random variable with mean 0 and unit variance. In addition to this intrinsic noise, it is reasonable to assume random fluctuations in the ants’ behavior due to individual variations, additional (random) interactions between colony members, physical limitations of their sensory systems, and environmental influences. The behavioral fluctuations enter into the model as fluctuations of the model parameters during the course of an experiment. We can determine the influence of parameter fluctuations on  $p_i$  for fixed  $c_i$  by the Delta-Method [6], which approximates the variance of a function  $f(X)$  of a random variable  $X$  with mean  $\mu_X$  and variance  $\sigma_X^2$  as  $\text{Var}(f(X)) = (\frac{d}{dx} f(\mu_X))^2 \sigma_X^2$ . It is easy to verify that even small fluctuations in  $\alpha$  have significant influence on

$p_i$ , especially when  $c_1$  is close to the unstable fixpoint (the decision point). We could endeavor to model the noise precisely using the Delta-Method for all rate constants in Eq. 1. However, this would be a very treacherous form of precision given that all model parameters are only estimates, that the basic model itself is only an approximation and that many other environmental factors can cause fluctuations. A good and simple approximation of the experimental data is to set  $\sigma$  to an appropriately fitted constant. We substitute  $p_i$  with  $(p_i + \sigma W)$  in the basic model equation and write the result formally as a diffusion in the form of an Itô stochastic differential equation where  $\mu(x)$  describes the deterministic development and  $\sigma dW$  describes the influence of noise [12].

$$dx = \mu(x)dt + \sigma dW \quad (2)$$

$$\mu(x) = Q_1 \frac{(k+x)^2}{(k+x)^2 + (k + \frac{Q_1 Q_2 - Q_2 x}{Q_1})^2} - \rho x \quad (3)$$

## 5 Fokker-Planck Analysis of Itô Diffusion Model

We have obtained the Itô diffusion Eq. (2,3) as our basic model for the pheromone level on the longer branch, where  $\sigma$  is a constant noise level. We are mainly interested in the steady-state pheromone levels. Instead of just a mean, the model allows us to obtain an explicit density function  $\pi(c)$  for the probability to find a pheromone level  $c$  on the longer branch after the system has run for a long time. Let  $f(t, y)$  be the probability density for the longer branch to carry  $y$  units of pheromone at time  $t$ . The time-development of  $f(\cdot, \cdot)$  is described by the Fokker-Planck Equation (FPE [18]).

$$\partial_t f(t, y) = -\partial_y [\mu(y) f(t, y)] + \partial_{yy} \left[ \frac{1}{2} \sigma^2(y) f(t, y) \right] \quad (4)$$

The steady state  $\pi(c) = f(c, t)$  is time-independent, so Eq. 4 reduces to an ODE

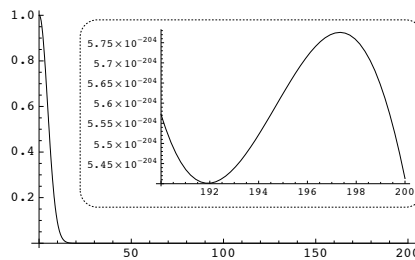
$$0 = -\frac{d}{dy} [\mu(y) \pi(y)] + \frac{1}{2} \frac{d^2}{dy^2} [\sigma^2(y) \pi(y)] \quad (5)$$

Since the pheromone level on the longer branch is physically limited to the interval  $(0, Q_1/\rho)$ , we must assume reflecting boundaries at both interval ends which prevents  $x$  from becoming negative and implies zero net flow of probability across the interval boundaries. The solution of Eq. 5 then is

$$\begin{aligned} \psi(x) &= e^{\int_a^x (2\mu(y)/\sigma^2(y)) dy} \\ \pi(x) &= C \frac{\psi(x)}{\sigma^2(x)} \end{aligned} \quad (6)$$

where  $C$  is a suitable normalization constant [12]. We plot the solution of Eq. 6 for  $q_1 < q_2$  in Fig. 6 (here,  $q_1/q_2 = 1/3$ ). Obviously, the vast majority of the probability mass is assigned to the vicinity of zero. The interpretation of this is that in the long run all pheromone will almost certainly vanish from the longer branch, provided both branches are available. Regardless of the start state of the system, the long branch will always be disused and the exploitation will switch back to the shorter (better) branch. This is indeed what we see in the *P. megacephala* experiments. However, our model must be able to account for both types of behavior, where the switching takes place and where it does not occur.

By inspection of the drift term  $\mu(x)$  in Fig. 5 we may suspect that something special is happening in the range of the upper limit of  $c_1$ . We magnify the range of the saturation level of  $c_1$  in the inset of Fig. 6 and observe a (tiny) local maximum of probability. The key to why this local maximum explains both cases is that the stationary distribution is only reached after infinite time. To know how long it will take for



**Fig. 6.** Stationary Distribution  $\pi$

the colony to disuse the longer branch after the shorter branch is reopened, we must find the expected time that it takes for the system to reach a very low pheromone level on the longer branch after starting it with the longer branch being (almost) completely saturated. This expected time is given by the so-called “First Passage Time” which can be obtained by solving the Kolmogorov-Backward Equation [12] for Eq. 2. For a reflecting boundary at the upper end  $b$  of the interval, the expected time  $t(x)$  for the pheromone level on the longer branch to fall from  $x$  to  $a$  is

$$t(x) = \int_a^x \left( \frac{2}{\psi(y)} \int_y^b \frac{\psi(z)}{\sigma^2(z)} dz \right) dy \quad (7)$$

The numeric solution to Eq. 7 for  $a = 100$  (in minutes) is plotted on the left in Fig. 7 for a variance of 0.04 which is approximately matched to our experiments for the 30 minutes before switching to Phase 3 ( $k = 16$  for *P. megacephala*). We note that this escape time is short, so we expect the pheromone level on the longer branch (and thus the number of foragers) to fall of relatively quickly, exactly as observed in the experiments. In the experiments with *L. niger* we see significantly lower noise levels [11]. Solving Eq. 7 for such low levels, we find that the escape time is dramatically higher (Note the scale in Fig. 7, right). We would thus not expect to see such a switch happen in real experiments or only in very rare cases. This is consistent with all experiments and demonstrates that the same stochastic model explains the *P. megacephala* experiments where the switch does happen and the *L. niger* experiments, where it is not observed.

To verify our findings we have implemented an individual-based simulation of the *P. megacephala* experiments (Java code can be obtained by request from the first author). Our model represents each ant in the colony as an individual



**Fig. 7.** Escape Time. left:  $\sigma^2 = 0.04$ , *P. megacephala*, right:  $\sigma^2 = 0.002$  *L. niger*

object. All actions are controlled with probabilistic decisions independently for each object, including resting, feeding, leaving the nest, moving and branch choice. The individual-based model also includes details from which the analytic model abstracts, specifically deposit reduction over time and stochastic total flux, to validate that the inclusion of these factors does not influence our results. Parametric studies are in agreement with the analytic model and confirm that the qualitative behavior of the model does not depend on these factors.

## 6 Discussion and Conclusions

We have given experimental evidence for truly adaptive behavior in ant foraging for *P. megacephala*. This behavior is qualitatively different from the behavior of other species, specifically *L. niger*, and to the best of our knowledge this is the first report of evidence for fully adaptive foraging in ants. We note that *L. niger* is non-invasive and relies on permanent food sources, while *P. megacephala* is an invasive species and opportunistic feeder exploiting ephemeral sources.

Surprisingly no new functional mechanisms needed to be invoked to explain the adaptive behavior. Randomness in the decision making turned out to be the crucial factor that allows the self-organized process to be adaptive. The standard models for ant foraging are unable to capture this behavior because they are mean field descriptions. We have presented a new type of analytic model based on stochastic differential equations that explains this behavior. Our findings are confirmed by individual-based simulations.

On a more general level, our main finding is that noise can enable self-organizing systems to adapt readily to changing environments. While self-limiting positive feedback loops are a core mechanism for self-organizing group activities, randomness is the driving factor that allows such systems to be adaptive. As always, there is a price to be paid: higher noise levels result in less efficient decision making in static environments. Cost and benefit of noise must thus be balanced. One could come to the bold conjecture that each ant species should have evolved to the optimum noise level for its typical environment. For example, when food patches differ little in quality, adaptiveness may not be required and less noise in the system would allow a quick and committed decision, i.e. generally more efficient foraging. On the other hand, when sources with large quality differences occur, it may be advantageous to use more noise in the system to be able to compare a new find to the currently used source. The slightly decreased general efficiency will be more than compensated for by the ability to adapt.

Our results are not only interesting in the context of natural systems but may have far reaching implications for applications of swarm intelligence [2]. Ant Colony Optimization algorithms, for example, are very directly modelled on the foraging behavior of real ants [3]. For some algorithms the resemblance is so close that the algorithms' function can fundamentally be understood as a simulation of ant foraging in an abstract phase space, and the fundamental model equations describing the algorithms' dynamic are virtually identical to those for real ant colonies. We may thus expect the behavior of these systems to be governed by the same rules. Similar considerations hold for swarm robots [2], self-organized routing algorithms [10], and other applications of swarm intelligence. Our results

indicate that noise should be taken into account as a constructive component when engineering such systems. For example, we may wish to use controlled injection of noise to trigger adaptation when the environment changes.

Systems of coupled feedback equations comparable to those used in ant foraging models are very common across a large variety of models for self-organized behavior and decision making. For example, the development of market trends [20] or the dispersion of innovations [5] can be modelled in this form. In consequence it is highly likely that here, too, we will need stochastic models to fully understand the characteristics of these mechanisms in dynamic environments. For one case we have demonstrated how this can be achieved using stochastic differential equations and Fokker-Planck equations. We are confident that this class of models has wide applicability to other self-organizing systems.

## References

1. R. Beckers, J.L. Deneubourg, and S. Goss. Modulation of trail laying in the ant *Lasius niger* and its role in the collective selection of a food source. *Journal of Insect Behaviour*, 6:751–759, 1993.
2. E. Bonabeau, M. Dorigo, and G. Theraulaz. *Swarm Intelligence—From Natural to Artificial Systems*. Oxford University Press, 1999.
3. E. Bonabeau, M. Dorigo, and G. Theraulaz. Inspiration for optimization from social insect behaviour. *Nature*, 406:39–42, 2000.
4. S. Camazine et al. *Self-Organization in Biological Systems*. Princeton University Press, 2001.
5. V. Capasso and D. Bakstein. *An Introduction to Continuous-Time Stochastic Processes*. Birkhäuser, 2005.
6. G. Casella and R.L. Berger. *Statistical Inference*. Duxbury, 2nd edition, 2002.
7. J.L. Deneubourg, J.M. Pasteels, and J.C. Verhaeghe. Probabilistic behavior in ants: A strategy of errors. *Journal of Theoretical Biology*, 105:259–271, 1983.
8. J.L. Deneubourg et al. The self-organizing exploratory pattern of the argentine ant. *Journal of Insect Behaviour*, 3:159–168, 1990.
9. C. Devigne and C. Detrain. How does food distance influence foraging in the ant *Lasius niger*. *Insectes Sociaux*, 53:46–55, 2006.
10. F. Dressler. *Self-Organization in Sensor and Actor Networks*. John Wiley, 2008.
11. A. Dussutour, J.-L. Deneubourg, and V. Fourcassié. Amplification of individual preferences in a social context: the case of wall-following in ants. *Proceedings of the Royal Society London B*, 272:705–714, 2005.
12. C.W. Gardiner. *Handbook of Stochastic Methods*. Springer-Verlag, 2004.
13. S. Garnier, J. Gautrais, and G. Theraulaz. The biological principles of swarm intelligence. *Swarm Intelligence*, 1:3–31, 2007.
14. B. Hölldobler and E.O. Wilson. *The Ants*. Springer-Verlag, 1990.
15. B. Meyer. On the convergence behaviour of ant colony search. In *Asia-Pacific Conference on Complex Systems*, Cairns, December 2004.
16. G. Nicolis and I. Prigogine. *Exploring Complexity*. W.H. Freeman, 1989.
17. S.C. Nicolis and J.L. Deneubourg. Emerging patterns and food recruitment in ants: an analytical study. *Journal of Theoretical Biology*, 198:575–592, 1999.
18. H. Risken. *The Fokker-Planck Equation*. Springer-Verlag, 1989.
19. D.J.T. Sumpter. The principles of collective animal behaviour. *Philosophical Transactions of the Royal Society B*, 361(1465):5–22, 2003.
20. G. Weisbuch and D. Stauffer. Hits and flops dynamics. *Physica A*, 287:563–576, 2000.