UCLA
UCLA Previously Published Works

Title
Spatiotemporal chemotactic model for ant foraging

Permalink
https://escholarship.org/uc/item/463363k6

Journal
Modern Physics Letters B, 28(30)

ISSN
0217-9849

Authors
Ramakrishnan, Subramanian
Laurent, Thomas
Kumar, Manish
et al.

Publication Date
2014-12-10

DOI
10.1142/s0217984914502388

Peer reviewed

World Scientific
www.worldscientific.com

Spatiotemporal chemotactic model for ant foraging

Subramanian Ramakrishnan

Department of Mechanical and Industrial Engineering,
University of Minnesota Duluth, Duluth, MN 55812, USA
sramakri@d.umn.edu

Thomas Laurent

Department of Mathematics, Loyola Marymount University,
Los Angeles, CA 90045, USA
tlaurent@lmu.edu

Manish Kumar

Department of Mechanical, Industrial and Manufacturing Engineering,
University of Toldeo, Toledo, OH 43606, USA
manish.kumar2@utoledo.edu

Andrea L. Bertozzi

Department of Mathematics, University of California-Los Angeles,
Los Angeles, CA 90095, USA
bertozzi@math.ucla.edu

In this paper, we present a generic theoretical chemotactic model that accounts for certain emergent behaviors observed in ant foraging. The model does not have many of the constraints and limitations of existing models for ants colony dynamics and takes into account the distinctly different behaviors exhibited in nature by ant foragers in search of food and food ferrying ants. Numerical simulations based on the model show trail formation in foraging ant colonies to be an emergent phenomenon and, in particular, replicate behavior observed in experiments involving the species *P. megacephala*. The results have broader implications for the study of randomness in chemotactic models. Potential applications include the developments of novel algorithms for stochastic search in engineered complex systems such as robotic swarms.

Keywords: Ant foraging; self-organization; complex systems; Keller–Segel model; chemotaxis.

Self-organizaton in biological systems such as bumble bees[1] and ant colonies,[2] in addition to being of theoretical interest, is important for the realization of engineered complex systems inspired by natural systems. *Trail formation in ant colonies foraging for food is an interesting example of self-organization.* Theoretical models of ant colonies foraging for food often assume the existence of a discrete number of trails between the nest and the food sources and focus on the evolution of the chemoattractant (pheromone) concentration along those trails.[3–6] However, the theory fails to explain many of the observed features of ant foraging and does not:

(i) allow for unconstrained exploration of the entire domain by the foragers resulting in trail formation realized as an emergent phenomenon,

(ii) account for the formation of a discrete number of trails, and

(iii) differentiate between foraging ants (which do not deposit pheromone) and food ferrying ants which contribute to the pheromone gradient.

Here we introduce a chemotactic model for ant foraging and demonstrate using numerical simulations that the model yields all of the above. In particular, the results reported in this paper account for the adaptive switching between trails observed in experiments involving the species *P. megacephala*.[2,7] The model and the results are relevant to the study of emergent phenomena in chemotactic biological and social systems. In addition, the present effort is expected to play a significant role in the development of stochastic search algorithms. Such algorithms are essential precursors to realizing robotic swarm systems with self-organizing capabilities.[8–11]

While foraging, initially ants emerge from the nest and locate food sources based on a stochastic exploration of the environment. They then return to recruit additional foragers while depositing pheromone as a navigational aid for the latter.[12,13] The process repeats itself with the strength of pheromone along a given trail indicating the desirability of the food source at the terminus. Various aspects of trail formation have been studied in the literature.[12,14–19] A basic question is how efficiently can ant colonies adapt to the discovery of new food sources while traffic patterns have already been established between the nest and existing ones. Many species do not exhibit appreciable levels of adaptability in laboratory experiments. For instance, the species *Lasius niger* failed to alter trails in response of the introduction of short cuts to the food sources.[20]

However, results from experiments involving the invasive species *P. megacephala* (Fig. 1) challenge the conclusion of weak adaptability.[2,7] The colony was allowed in the first phase to forage for an hour toward two food sources configured in a Y-bridge framework at unequal distances from the nest and a stronger trail was established toward the nearer food source. In the second phase, traffic to the closer food source (short branch) was blocked for an hour thereby allowing the traffic to strongly shift toward the farther food source (long branch). When the short branch was unblocked in the third phase, the ants adapted remarkably to the change and the nearer food source was, once again, established as the preferred one. The results of repeated trials indicate that, statistically, the species is very likely to exhibit
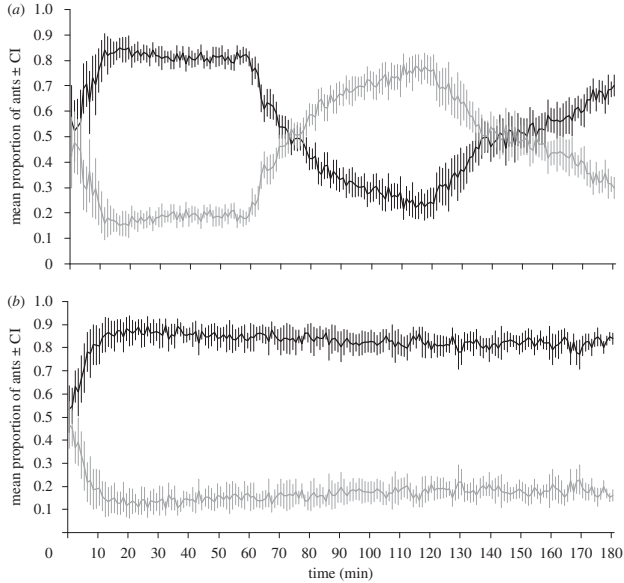
Fig. 1. Traffic along two ant trails: (a) short branch (to favorable food source) blocked and re-opened, and (b) both branches unchanged. Black line, short branch; light grey line, long branch (figure from Ref. 2).

the aforementioned dynamic switching, which is clearly observed in Fig. 1(a). In contrast, Fig. 1(b) represents the traffic pattern in the case where traffic to the favorable food source was not blocked at all.

We now ask whether the behavior reported in Refs. 2 and 7 may be explained analytically? Mathematical models of foraging typically assume that a fixed number of trails exist and focus on pheromone evolution given by $\frac{dc_i}{dt} = p_i \Lambda q_i - \mu c_i$,[14] where c_i denotes the pheromone concentration along trail i, p_i is the probability of trail i being chosen, Λ is the constant, total flux of foragers, q_i is the amount of pheromone deposited by an individual forager and μ is the constant evaporation rate of pheromone. The important question of the formation of the trails themselves lies outside the scope of such models. Stochastic extension of the above equations for the case of two trails is considered in Ref. 2 and noise induced transitions between equilibrium points is suggested as the mechanism that causes the switching behavior. A reaction-diffusion model for random walkers driven by chemotaxis has been considered in Ref. 21.

However, these approaches fail to make the crucial distinction between foraging ants (which do not deposit any pheromone) and the nest-seeking ants (which deposit pheromone). It is also unclear whether such models can explain the emergent behavior reported in Refs. 2 and 7. We note that pattern formation, qualitatively similar to trail formation in ants, has been discussed in other contexts such as territorial pattern formation in wolves wherein the existence and extent of wolf

territory and buffer zones are shown to emerge as stable steady state solutions to the dynamical equations.[22]

We now present our model. Consider an ant colony engaged in two distinct types of behaviors: (i) searching for food or foraging, and (ii) food carrying or "nest-seeking". Food search is governed by an environmental potential, the pheromone gradient, and is also characterized by inherent randomness that allows for a search of the entire domain for food sources. We also account for the fact that a fraction of the foraging ants change character to food carrying ants within a certain neighborhood of the food sources and the reverse happens within a neighborhood of the nest. Consider the nest Ω_N and k food sources denoted by $\Omega_{F_1}, \Omega_{F_2}, \ldots, \Omega_{F_k}$. Denoting the density of ants engaged in food search by ρ_0, the densities of the food carrying ants from the k food sources by ρ_i ($i = 1, 2, \ldots, k$), the pheromone density by c, the conversion factor from foraging to nest seeking at food source i by α_i and the reverse conversion factor at the nest by β, we propose the following equations for our diffusive model:

$$\frac{\partial \rho_0}{\partial t} + \text{div}(\rho_0 \nabla c) = \Delta \rho_0 - \sum_{i=1}^{k} (\alpha_i \chi_{\Omega_{F_i}}) \rho_0 + \beta \chi_{\Omega_N} \sum_{i=1}^{k} \rho_i \,,$$

$$\frac{\partial \rho_i}{\partial t} + \text{div}(\rho_i \nabla \Phi) = \alpha_i \chi_{\Omega_{F_i}} \rho_0 - \beta \chi_{\Omega_N} \rho_i; \quad i = 1, \ldots, k \,, \tag{1}$$

$$\frac{\partial c}{\partial t} = \Delta c - c + \sum_{i=1}^{k} \gamma_i \rho_i \,.$$

In the above equations, $\chi_{\Omega_{F_i}}$ and χ_{Ω_N} represent characteristic functions that vanish outside of the respective domains around the food sources and the nest where the type conversions occur. Only the nest seeking ants contribute to the pheromone density.

Experiments show that (see e.g. species *Lasius niger*[16]) ants returning to the nest tend to deposit more pheromone closer to the food sources. Accordingly, the rate of deposition of pheromone by ants returning from a food source i [given by γ_i in Eq. (1)] is a decreasing function of the distance s from the food source. In the simulation results reported below we have employed the function $\gamma(s) = \frac{1}{1+s}$. The potential Φ is chosen to be $\Phi(\mathbf{x}) = |\mathbf{x} - \mathbf{x}_N|$, where $\mathbf{x}_N$ is the barycenter of the nest domain Ω_N. Thus, the velocity of the food carrying ants is normalized in magnitude unity and oriented towards x_N at all times *as suggested by natural observations*.[23] We note here that the equations of the Keller–Segel model of chemotaxis[24] exhibit mathematically singular behavior including the divergence of the population density in finite time (see, for instance, Ref. 25). Considering foraging ants and food carrying ants as distinct populations characterized by distinct densities appears to prevent the emergence of finite time singularities in our model. Hence, the model equations remain valid for all times in the evolution.

We now present simulation results considering the 1D case first. Here the nest is located at $x = 50$ and the two food sources are at 1: $x = 70$ and 2: $x = 26$, respectively. The simulation is run for a total time period of 8000 units. We measure temporal and spatial intervals in non-dimensionalized units. The ant density is simulated using the particle method considering a total number of 400 agents, wherein the density of ants is discretized using 400 particles (representing the ants) and each particle obeys the (stochastic) ordinary differential equation underlying the partial differential equation (see, for instance, Ref. 26 for more details on the particle method). The values of $\alpha_i = 0.99 \ \forall i$ and $\beta = 0.99$ are chosen to represent the conversion factors in the simulations, thereby allowing a very small fraction of the foragers to not get converted to nest-seeking ants at once.

Pheromone density is simulated using the finite difference method over the 1D mesh of size 1000 corresponding to the domain of size 100. Similar to the experiments,[2,7] food source 1 is eliminated at time $t = 3000$ units and re-introduced at $t = 5000$ units. Figure 2 (top) shows how the number of ants visiting both the food sources evolves in time. The time evolution of the corresponding pheromone density is shown in Fig. 3, in a clockwise manner, for time instants $t = 0$, $t = 3000$, $t = 5000$ and $t = 8000$ units. Initially, the agents stochastically explore the domain and conclude that food source 1 is more favorable, as indicated by the significantly higher pheromone density around that food source (see the top right sub-figure in Fig. 3). The density around food source 2 increases sharply once food source 1 is eliminated (bottom left sub-figure in Fig. 3). The favorability of food source 1 is re-established once the former is reintroduced into the domain (bottom right
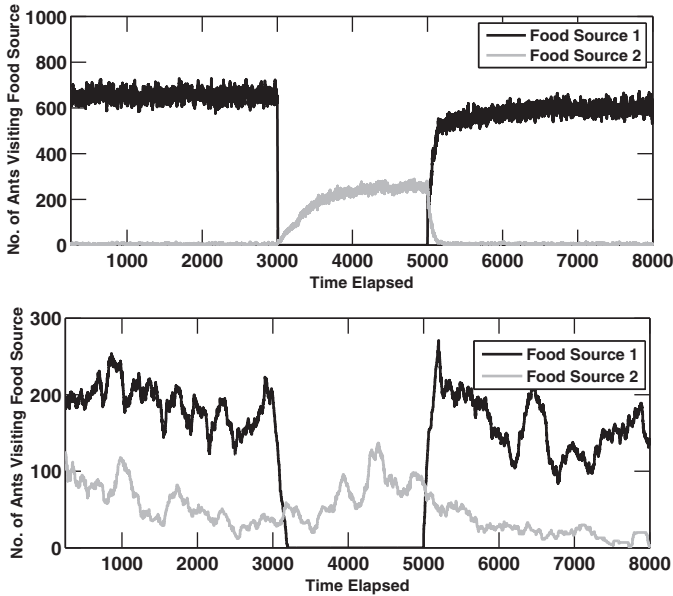

Fig. 2.   Number of ants visiting each food source: 1D case (top) and 2D case (bottom).
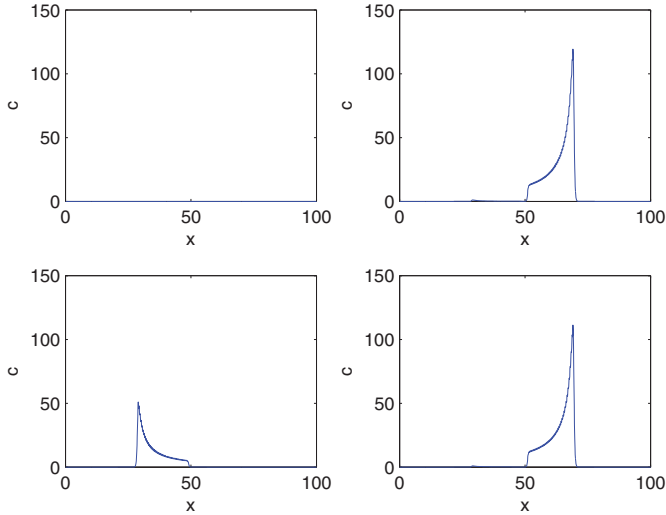
Fig. 3.   1D case: Pheromone density (c) plotted with respect to the location (x) of the nest and food sources at: $t = 0$ (top left); $t = 3000$ (top right); $t = 5000$ (bottom left); and $t = 8000$ (bottom right).

sub-figure in Fig. 3). The results presented in Figs. 2 (top) and 3 confirm not only the formation of the dominant trail to the favorable food source,but also the adaptive switching behavior that *emerges* from the model.

We now present results for the 2D case. Simulations are run for 8000 time units with the nest at coordinates $(50, 30)$ and two food sources at 1: $(70, 50)$ and 2: $(25, 50)$. The values of $\alpha_i = 0.99 \ \forall i$ and $\beta = 0.99$ are chosen. The ant density is simulated using the particle method considering a total number of 400 agents. The pheromone density is simulated using the finite difference method over the 2D mesh of size 1000 by 1000 corresponding to a domain of size 100 by 100 units. Neumann boundary conditions are assumed throughout. Figure 2 (bottom) shows the number of ants visiting both the food sources as a function of time. Corresponding spatial distributions of pheromone are shown in Fig. 4 for time instants $t = 0$, $t = 200$, $t = 3000$, $t = 5000$, $t = 5200$, and $t = 8000$ units. The agents start off from the nest at time $t = 0$, and follow the dynamics governed by Eq. (1). Initial pheromone concentration is considered to be zero everywhere.

Consistent with the observed behavior seen in ant colonies, which favors closer food sources over the farther ones, it can be seen in Fig. 2 (bottom) that the traffic toward the first food source quickly becomes higher than the traffic towards the second food source. This is also evident in Fig. 4 (top right) which shows higher concentration of pheromone on the trail leading to food source 1. At time $t = 3000$ units, food source 1 is removed (note the sharp drop of the top curve in Fig. 2 (bottom) from $t = 3000$ since no ant is able to discover food source 1 after that time). Consequently, the traffic toward food source 2 picks up (the trajectory of
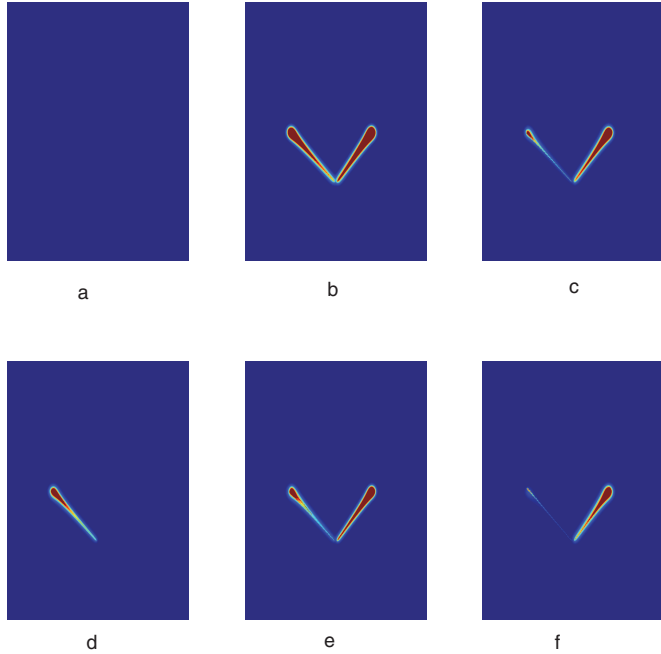
Fig. 4.   (Color online) 2D case: Pheromone density along trails at times: (a) $t = 0$; (b) $t = 200$; (c) $t = 3000$; (d) $t = 5000$; (e) $t = 5200$ and (f) $t = 8000$. The axes represent a 2D spatial domain.

the bottom curve after $t = 3000$ in Fig. 2 (bottom)) and the pheromone trail to this food source becomes strong as seen in Fig. 4 (bottom left). When food source 1 is re-introduced at $t = 5000$ units, the traffic toward food source 1 picks up (see Figs. 2 (bottom) and 4 (bottom center)) despite the fact that the pheromone trail has almost disappeared due to evaporation and diffusion. The snapshots of the pheromone trails presented in Fig. 4 is consistent with the above mentioned emergent dynamics. We now take a closer look. Starting off with no trails (top left), the favorability of food source 1 is eventually established (top right). Once food source 1 is eliminated at $t = 3000$, the trail to that food source vanishes almost entirely by $t = 5000$ (bottom left), at which point food source 1 is re-introduced. By $t = 5200$, the trail to food source 1 has re-emerged (bottom center) and becomes quite strong by $t = 8000$ (bottom right).

To obtain a direct comparison with the results of Refs. 2 and 7, we counted the total number of new ants visiting a given food site for a period of 200 units of time for the plots in Fig. 2 (bottom). Note that in contrast with the Y-bridge experiments,[2,7] in our simulations the agents are allowed unconstrained motion in a 2D environment. Comparing with Fig. 1, we observe a qualitative similarity between the experimental results and those obtained from our model.

We also note that while the number of ants visiting food source 1 vanishes after the food source is removed in the simulations, it never quite goes to zero in the

experiments. We believe this to be a consequence of the characteristic time scale inherent to the problem. Given enough time after a food source is removed, the average number of ants visiting that food source may vanish. However, the central point of the result obtained for the 2D case in Fig. 2 (bottom) is that, when reintroduced, food source 1 regains its favorable status. This follows purely from the dynamics of the model.

In conclusion, in this paper, we introduced a spatiotemporal chemotactic model for ant foraging that represents a significant improvement over existing models. The model distinguishes between foraging ants and food-carrying ants. The foraging ants initially explore the entire domain and are guided during later times by the pheromone concentration as traffic gets established between discovered food sources and the nest. Only the food-carrying ants contribute to the pheromone density. The model allows for conversions between the two types of ants within well defined neighborhoods of the food sources and the nest and appears to be free of finite time singularities that arise in the classical Keller–Segel model. Numerical simulation results based on the model, in addition to demonstrating the emergence of trails, account for adaptive behavior observed in experiments involving the species *P. megacephala*.

Several aspects need further investigation. For instance, sensitivity of the results and bifurcations with respect to parameters such as the diffusion coefficients of foraging ant density and pheromone as well as the evaporation coefficient (all of which have been normalized to unity in Eq. (1)) is an important question. Asymptotic behavior of the solutions is yet another interesting aspect. This model can be extended to study the adaptive self-organizing behaviors observed in ants when the food sources are depleting in nature. Moreover, another interesting extension of the model would be to study different types of noise models (of the non-Brownian type) and their effecst on the efficiency of foraging. From a practical standpoint, self-organization experiments using mobile robots with stochastic search algorithms based on the model would be of interest in robotic applications.

Acknowledgments

References

1. F. Lenz, T. C. Ings, L. Chittka, A. V. Chechkin and R. Klages, *Phys. Rev. Lett.* **108** (2012) 098103.
2. A. Dussutour, M. Beekman, S. C. Nicolis and B. Meyer, *Proc. Roy. Soc. B* **276** (2009) 4353.
3. A. Dussutour, V. Fourcassie, D. Helbing and J. L. Deneubourg, *Nature* **428** (2004) 70.
4. S. C. Nicolis and J. L. Deneubourg, *J. Theor. Biol.* **198** (1999) 575.
5. K. Johnson and L. F. Rossi, *J. Theor. Biol.* **241** (2006) 360.
6. L. Edelstein-Kesht, *J. Math. Biol.* **32** (1994) 303.
7. B. Meyer, in *Proc. Second IEEE Int. Conf. Self-Adaptive and Self-Organizing Systems*, eds. S. Breuckner, P. Robertson and U. Bellur (IEEE Computer Society, Los Alamitos, CA, 2008), pp. 435–444.
8. M. J. B. Krieger, J. B. Billeter and L. Keller, *Nature* **406** (2000) 992.
9. C. R. Kube and H. Zhang, *Adapt. Behav.* **2** (1994) 189.
10. E. Bonabeau, M. Dorigo and G. Theraulaz, *Swarm Intelligence: From Natural to Artificial Systems* (Oxford University Press, 1999).
11. E. Bonabeau, M. Dorigo and G. Theraulaz, *Nature* **406** (2000) 39.
12. B. Holldobler and E. O. Wilson, *The Ants* (Belknap Press of Harvard University, 1990).
13. I. D. Couzin, *Trends Cogn. Sci.* **13** (2009) 36.
14. J. L. Deneubourg, S. Aron, S. Goss and J. M. Pasteels, *J. Insect Behav.* **3** (1990) 159.
15. K. Vittori, G. Talbot, J. Gautrais, V. Fourcassie, A. F. R. Araujo and G. Theraulaz, *J. Theor. Biol.* **239** (2006) 507.
16. R. Beckers, J. L. Deneubourg and S. Goss, *J. Insect Behav.* **6** (1993) 751.
17. J. C. de Biseau and J. M. Pasteels, *J. Insect Behav.* **7** (1994) 767.
18. M. Beekman, D. J. T. Sumpter and F. L. W. Ratneiks, *Proc. Natl. Acad. Sci. USA* **98** (2001) 9703.
19. D. E. Jackson and N. Chaline, *Animal Behav.* **74** (2007) 463.
20. R. Beckers, J. L. Deneubourg, S. Goss and J. M. Pasteels, *Insect Soc.* **37** (1990) 258.
21. F. Schweitzer and L. Schimansky-Geier, *Physica A* **206** (1994) 359.
22. M. A. Lewis and J. D. Murray, *Nature* **366** (1993) 23.
23. M. Muller and R. Wehner, *Proc. Natl. Acad. Sci. USA* **85** (1988) 5287.
24. E. F. Keller and L. A. Segel, *J. Theor. Biol.* **30** (1971) 225.
25. A. Blachet, J. Dolbeault, and B. Perthame, *Elec. J. Diff. Eqs.* **44** (2006) 1.
26. R. Camassa, P. H. Chiu, L. Lee and T. W. H. Sheu, *Commun. Pure Appl. Anal.* **10** (2011) 1503.