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Biomimicry of Social Foraging Bacteria for Distributed Optimization: Models, Principles, and Emergent Behaviors[1]

Y. Liu[2] and K. M. Passino[3]

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Abstract. In this paper, we explain the social foraging behavior of E. coli and M. xanthus bacteria and develop simulation models based on the principles of foraging theory that view foraging as optimization. This provides us with novel models of their foraging behavior and with new methods for distributed nongradient optimization. Moreover, we show that the models of both species of bacteria exhibit the property identified by Grunbaum that postulates that their foraging is social in order to be able to climb noisy gradients in nutrients. This provides a connection between evolutionary forces in social foraging and distributed nongradient optimization algorithm design for global optimization over noisy surfaces.

Key Words. Distributed optimization, biomimicry, bacteria, models.

1. Introduction

Natural selection tends to eliminate animals with poor foraging strategies (methods for locating, handling, and ingesting food) and favor the propagation of genes of those animals that have successful foraging strategies, since they are more likely to enjoy reproductive success (they obtain enough food to enable them to reproduce). After many generations, poor foraging strategies are either eliminated or shaped into good ones (redesigned). Logically, such evolutionary principles have led scientists in the field of foraging theory to hypothesize that it is appropriate to model the activity of foraging as an optimization process: a foraging animal takes

[1]This work was supported in part by the DARPA/MICA Program.
[2]PhD Student, Department of Electrical Engineering, Ohio State University, Columbus, Ohio.
[3]Professor, Department of Electrical Engineering, Ohio State University, Columbus, Ohio.

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actions to maximize the energy obtained per unit time spent foraging, in the face of constraints presented by its own physiology (e.g., sensing and cognitive capabilities) and environment (e.g., density of prey, risks from predators, physical characteristics of the search area). Evolution has balanced these constraints and essentially engineered what is sometimes referred to as an optimal foraging policy (such terminology is especially justified in cases where the models and policies have been ecologically validated). Optimization models are also valid for social foraging where groups of animals communicate to cooperatively forage.

Foraging can be modeled as an optimization process where an animal seeks to maximize the energy obtained per unit time spent foraging. We begin by overviewing the relevant research in foraging theory, foraging by communicating organisms (social foraging) which sometimes operate in swarms, and the relevance of these areas to optimization. Next, we provide a brief literature overview of the area of bacterial foraging as it forms the biological foundation for this paper.

Foraging theory is described in Ref. 1. Animal behavior, including foraging theory and its ecological validity is discussed in Ref. 2 and the behavioral ecology of finding resources is discussed in Ref. 3. The view that social foraging evolved for improving climbing of noisy gradients of nutrient resources is introduced in Ref. 4. Group behavior of organisms is discussed in the areas of swarm intelligence and artificial life (Refs. 5–8). Ant colony optimization is an optimization method based on foraging in ant colonies and is discussed in Ref. 5 (the discussion on the Argentine ants was taken from Ref. 9). There, the focus is on biomimicry for solution of combinatorial optimization algorithms (e.g., shortest path algorithms). An overview of the biology and behavioral ecology of swarms is given in Ref. 10. A relevant book on self-organization in biological systems is Ref. 11, and this book discusses also foraging of several types of organisms, synchronization of fire fly flashing, and other types of self-organization properties of groups of organisms (e.g., construction of structures such as honeycombs).

In this paper, we adopt the optimal foraging theory perspective in formulating our computer simulation models. We validate the models and show that the principle of climbing noisy gradients introduced in Ref. 4 is valid for both models and species of bacteria, something that has not been done in the literature (e.g. in Refs. 12–14).

The description of the biological details of the E. coli bacteria and their motile behavior in this paper was taken from Refs. 15–21. Pattern formation in E. coli and S. typhimurium is discussed in Refs. 22–27; a mathematical swarm model and simulations are provided in Ref. 25. An overview of tactic responses that was used to explain the motile behavior of bacteria other than E. coli is given in Ref. 26.

Motile behavior of bacterial swarms of M. xanthus and some related bacteria are described in Refs. 26 and 28–30. A swarm motility model for M. xanthus that is based on a high-frequency gene mutation called the "Pied piper model" is given in Refs. 31–32; computer simulations of some aspects of this model are given in Ref. 32. Simulations of myxobacteria based on a stochastic cellular automata approach are described in Refs. 13–14.

Finally, we note that the conjugation of bacteria has been modeled in genetic algorithms and used for optimization (Ref. 33). There, taxes and foraging were not considered, just the particular mechanism of sex for gene transfer and how this impacts the optimization process of the genetic algorithm.

Here, our models for the social foraging are different from past ones. For example, we model more details of the social foraging of E. coli than in Ref. 12 (e.g., the effect of nutrient concentration on intercell communications). For M. xanthus, we model all aspects of the life cycle of the cell, unlike in Refs. 13–14 where only certain aspects are considered. Moreover, we provide links between the two models via showing that they both illustrate the Grunbaum concept of climbing noisy gradients.

The optimization methods introduced in this paper can be classified as distributed nongradient optimization methods. While genetic algorithms can solve similar optimization problems, their structure and operation is quite different. A good introduction to deterministic nongradient methods for optimization is given in Refs. 34–35. There are a variety of relevant optimization methods in the literature.

Here, we create simply optimization models of the social foraging of two species of bacteria. While, just like in Ref. 12, there is potential for application to engineering problems, and there may be benefits over existing optimization methods, it is beyond the scope of this paper to prove that this is the case (e.g., via theoretical convergence analysis or simulation benchmark studies). Indeed, there is ongoing research that is studying this now.

2. E. Coli: Optimization Model and Simulation Results

2.1. Modeling

2.1a. Foraging Theory. Animals search for and obtain nutrients in a way that maximizes the ratio E/T (where E is the energy obtained and T is the time spent foraging) or maximizes the long-term average rate of energy intake. Evolution optimizes the foraging strategies, since animals that have poor foraging performance do not survive.

Generally, a foraging strategy involves finding a patch of food (e.g., group of bushes with berries), deciding whether to enter it and search for

food, and when to leave the patch. There are predators and risks, energy required for travel, and physiological constraints (sensing, memory, cognitive capabilities). Foraging scenarios can be modeled and optimal policies can be found using, for instance, dynamic programming. Search and optimal foraging decision-making of animals can be broken into three basic types: cruise (e.g., tunafish, hawks), saltatory (e.g., birds, fish, lizards, and insects), and ambush (e.g., snakes, lions). In a cruise search, the animal searches the perimeter of a region; in an ambush, it sits and waits; in saltatory search, an animal typically moves in some directions, stops or slows down, looks around, and then changes direction (it searches throughout a whole region).

Some animals forage as individuals and others forage as groups. While to perform social foraging an animal needs communication capabilities, it can gain advantages in that it can exploit essentially the sensing capabilities of the group, the group can gang-up on large prey, individuals can obtain protection from predators while in a group, and in a certain sense the group can forage with a type of collective intelligence. Social foragers include birds, bees, fish, ants, wildbeasts, and primates. Note that there is a type of cognitive spectrum where some foragers have little cognitive capability and other higher life forms have significant capabilities (e.g., compare the capabilities of a single ant with those of a human). Generally, endowing each forager with more capabilities can help them succeed in foraging, both as an individual and as a group. From an engineering perspective, both ends of such a spectrum are interesting.

2.1b. Chemotactic Behavior of E. coli. Here, we consider the foraging behavior of E. coli, which is a common type of bacteria (it lives in your gut) with a diameter of $1\,\mu$m and a length of about $2\,\mu$m, and which under appropriate conditions can reproduce (split) in 20 min. Its ability to move comes from a set of up to six rigid 100–200 rps spinning flagella, each driven by a biological motor. An E. coli bacterium alternates between running (at 10–20 μm/sec, but they cannot swim straight) and tumbling (changing direction). When the flagella rotate clockwise (counterclockwise), they operate as propellers and hence an E. Coli may run or tumble.

Chemotactic Actions:

(A1) If in neutral medium, alternate tumbles and runs $\Rightarrow$ search.

(A2) If swimming up a nutrient gradient (or out of noxious substances), swim longer (climb up nutrient gradient or down noxious gradient) $\Rightarrow$ seek increasingly favorable environments.

(A3) If swimming down a nutrient gradient (or up noxious substance gradient), then search $\Rightarrow$ avoid unfavorable environments.

In this way, it can climb up nutrient hills and at the same time avoid noxious substances. The sensors it uses are receptor proteins which are very sensitive, and overall there is a high gain (i.e., a small change in the concentration of nutrients can cause a significant change in behavior). The sensor averages sensed concentrations and computes a time derivative. This is probably the best-understood sensory and decision-making system in biology (it is understood and simulated at the molecular level).

Bacteria are often killed and dispersed and this can be viewed as part of their motility. Mutations in E. coli affect, e.g., the reproductive efficiency at different temperatures, and occur at a rate of about 10^{-7} per gene and per generation. E. coli occasionally engage in a type of sex called conjugation that affects the characteristics of a population of bacteria. There are many types of taxes that are used by bacteria. For instance, some bacteria are attracted to oxygen (aerotaxis), light (phototaxis), temperature (thermotaxis), or magnetic lines of flux (magnetotaxis). Some bacteria can change their shape and number of flagella based on the medium to reconfigure so as to ensure efficient foraging in a variety of media.

E. coli and S. typhimurium can form intricate stable spatio-temporal patterns in certain semisolid nutrient media. They can eat radially their way through a medium if placed together initially at its center. Moreover, under certain conditions, they will secrete cell-to-cell attractant signals so that they will group and protect each other. These bacteria can swarm.

2.1c. Bacterial Swarm Foraging for Optimization. Here, the basic goal is to find the minimum of $J(\theta)$, $\theta \in R^p$, when we do not have the gradient $\nabla J(\theta)$. Suppose that θ is the position of a bacterium, and $J(\theta)$ represents an attractant-repellant profile; i.e., it represents where nutrients and noxious substances are located, so $J<0, J=0, J>0$ represent the presence of nutrients, a neutral medium, and the presence of noxious substances, respectively.

Let

$$P(j,k,l) = \{\theta^i(j,k,l) \,|\, i = 1, 2, \ldots, S\}$$

represent the positions of each member in the population of the S bacteria at the jth chemotactic step, kth reproduction step, and lth elimination-dispersal event. Let $J(i, j, k, l)$ denote the cost at the location of the ith bacterium $\theta^i(j,k,l) \in R^p$. Let N_c be the length of the lifetime of the bacteria as measured by the number of chemotactic steps. To represent a tumble, a unit length random direction, say $\phi(j)$, is generated; then, we let

$$\theta^i(j+1,k,l) = \theta^i(j,k,l) + C(i)\phi(j),$$

so that $C(i) > 0$ is the size of the step taken in the random direction specified by the tumble. If at $\theta^i(j+1, k, l)$ the cost $J(i, j+1, k, l)$ is better (lower) than at $\theta^i(j, k, l)$, then another chemotactic step of size $C(i)$ in this same direction will be taken and repeated up to a maximum number of steps N_s.

Let d_{attract} be the depth of the attractant released by the cell, and let w_{attract} be a measure of the width of the attractant signal. How does a cell repel another one? Via local consumption, and cells are not food for each other. Let $h_{\text{repellant}} = d_{\text{attract}}$ be the height of the repellant effect (magnitude), and let $w_{\text{repellant}}$ be a measure of the width of the repellant. Then, we may use functions $J_{cc}^i(\theta)$, $i = 1, 2, \ldots, S$, to model the cell-to-cell signaling via an attractant and a repellant. Let

$$J_{cc}(\theta) = \sum_{i=1}^{S} J_{cc}^i = \sum_{i=1}^{S} \left[-d_{\text{attract}} \exp\left(-w_{\text{attract}} \sum_{j=1}^{p} (\theta_j - \theta_j^i)^2 \right) \right] + \sum_{i=1}^{S} \left[h_{\text{repellant}} \exp\left(-w_{\text{repellant}} \sum_{j=1}^{p} (\theta_j - \theta_j^i)^2 \right) \right],$$

where $\theta = [\theta_1, \ldots, \theta_p]^T$ is a point on the optimization domain. The expression of $J_{cc}(\theta)$ implies that its value does not depend on the nutrient concentration at position θ. Actually, it is reasonable to assume that the depth of the chemical secreted by a bacterium is affected by environment; i.e., a bacterium with high nutrient concentration will secret stronger attractant than one with low nutrient concentration. In our model, we use the function $J_{ar}(\theta)$ to represent the environment-dependent cell-to-cell signaling. Let

$$J_{ar}(\theta) = \exp(M - J(\theta)) J_{cc}(\theta),$$

where M is a tunable parameter. Then, for swarming, we will consider minimization of $J(i, j, k, l) + J_{ar}(\theta^i(j, k, l))$, so that the cells will try to find nutrients, avoid noxious substances, and at the same time try to move toward other cells, but not too close to them.

Note the function $J_{ar}(\theta^i(j, k, l))$ implies that, with M being constant, the smaller $J(\theta)$, the larger $J_{ar}(\theta)$ and thus the stronger attraction, which is intuitively reasonable. In tuning the parameter M, it is normally found that, when M is very large, $J_{ar}(\theta)$ is much larger than $J(\theta)$ and thus the profile of the search space is dominated by the chemical attractant secreted by E. coli. On the other hand, if M is very small, then $J_{ar}(\theta)$ is much smaller than $J(\theta)$ and it is the effect of the nutrients that dominates. In $J_{ar}(\theta)$, we choose the scaling factor of $J_{cc}(\theta)$ as in exponential form, but this is not the only choice. Other functions which decrease monotonically and approach zero asymptotically are feasible candidates, though some additional constraints may be required.

After N_c chemotactic steps, a reproduction step is taken. Suppose there are N_{re} reproduction steps. For reproduction, the healthiest bacteria (the ones that have the lowest accumulated cost over their lifetime) split, and then we kill the same number of unhealthy ones (hence, we get a constant population size). Let N_{ed} be the number of elimination-dispersal events and, for each elimination-dispersal event, each bacterium in the population is subjected to elimination-dispersal (death, then random placement of a new bacterium at a random location on the optimization domain) with probability p_{ed}. Is this a biologically valid model? No, not completely. The objective is simply to capture the gross characteristics of chemotactic hill-climbing and swarming.

2.2. Simulation Results. As an illustrative example, we use our model to try to find the location with highest nutrient concentration on a certain map and show the results on Fig. 1. The nutrient map is constructed by summing up several Gaussian functions with different magnitude and variance. The contour plots of the map are shown in the figure, with the best

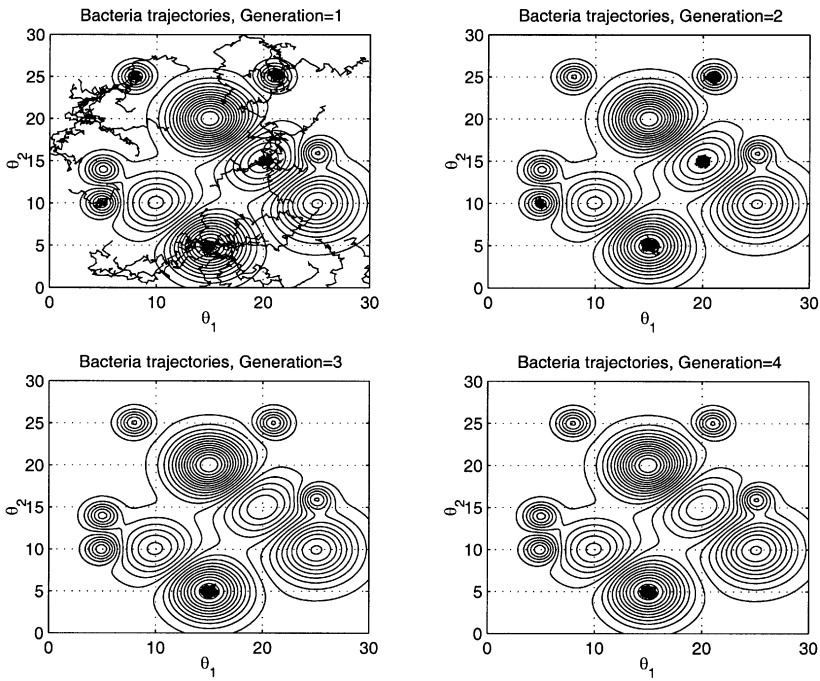

Fig. 1a. Foraging of E. coli with reproduction, elimination and dispersion: Contour plot before elimination and dispersion.

nutrient concentration located at $[15, 5]^T$. In this example, we include reproduction, elimination, and dispersion of E. coli and demonstrate the roles which these processes play in the E. coli evolution (Ref. 12). In the simulation, we choose $N_{re} = 4$ and $N_{ed} = 2$, which means that, during the simulation, E. coli evolve four generations and experience elimination and dispersal event once, respectively.

Initially, the bacteria are distributed randomly over the nutrient map. In Fig. 1a, we see that the first generation of E. coli are moving around to search for places with a better nutrient concentration, as shown by those curvy trajectories on the contour plot. In the second generation, almost all the bacteria have found such places, though all of them are not global optimal points. With evolution, all in the third generation find the position on the map with the best nutrient concentration, and the fourth generation stays there firmly. Simulation results in Fig. 1b are a continuation of Fig. 1a, but an elimination and dispersal process happens in between. In Fig. 1b, some bacteria of the first generation appear in some bad positions. But after

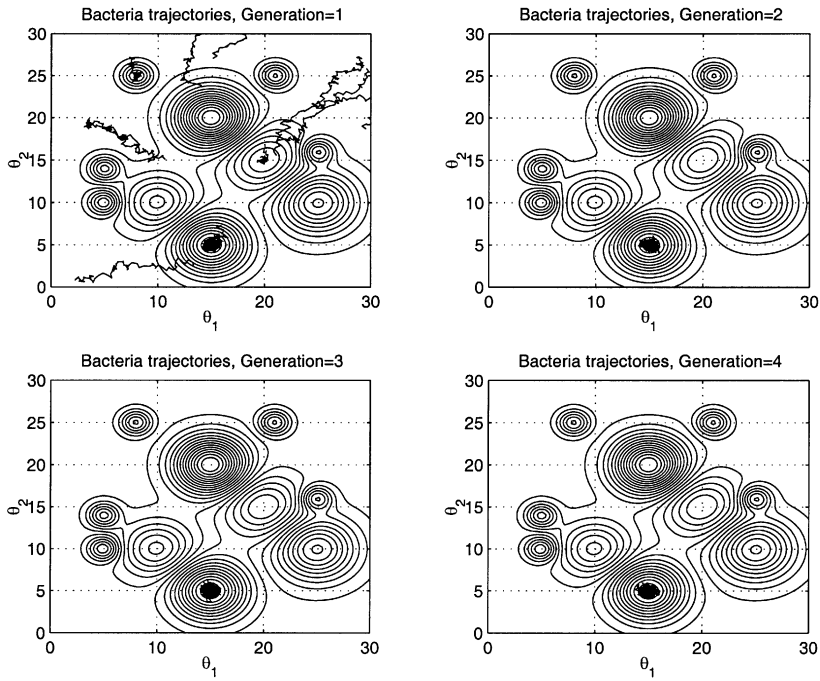

Fig. 1b. Foraging of E. coli with reproduction, elimination and dispersion: Contour plot after elimination and dispersion.

reproduction, almost all of the E. coli locate the global optimal position quickly and stay there from the second generation.

In the above example, we assume that the nutrient map is noise-free. But in reality, the environment is always noisy, which generally will prevent the individual bacterium from finding the optimal position. Next, with another simple example, we will illustrate that, by secreting chemicals, E. coli may swarm and perform social foraging. As a result, the bacteria may overcome the noise trap and pull each other into the optimal position. This was first discussed by Grunbaum (Ref. 4). Now, we will try to validate it by simulation.

In this case, we use a simple noise-contaminated quadratic nutrient profile with contour map shown on Fig. 2. The profile has the best nutrient concentration at $[15, 15]^T$. The simulation is run 300 steps. Figure 2a demonstrates the results when no chemical-attractant-induced swarming is present. Specifically, it shows the positions of the bacteria on certain chemotactic steps, where each + in the plots represents a bacterium. Obviously, lots of

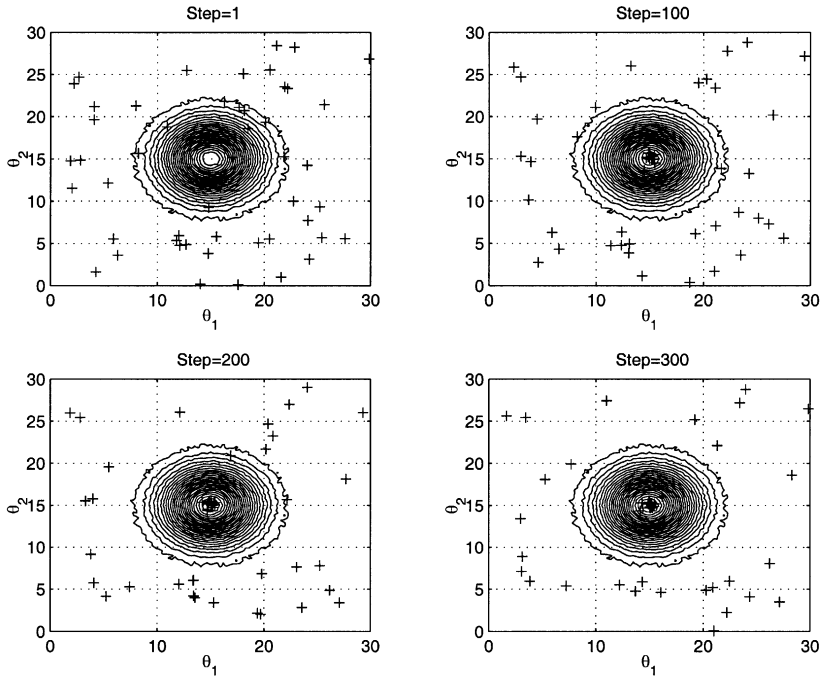

Fig. 2a. Foraging of E. coli in a noisy environment: Bacteria positions at different chemotactic steps (without cell-to-cell attractant).

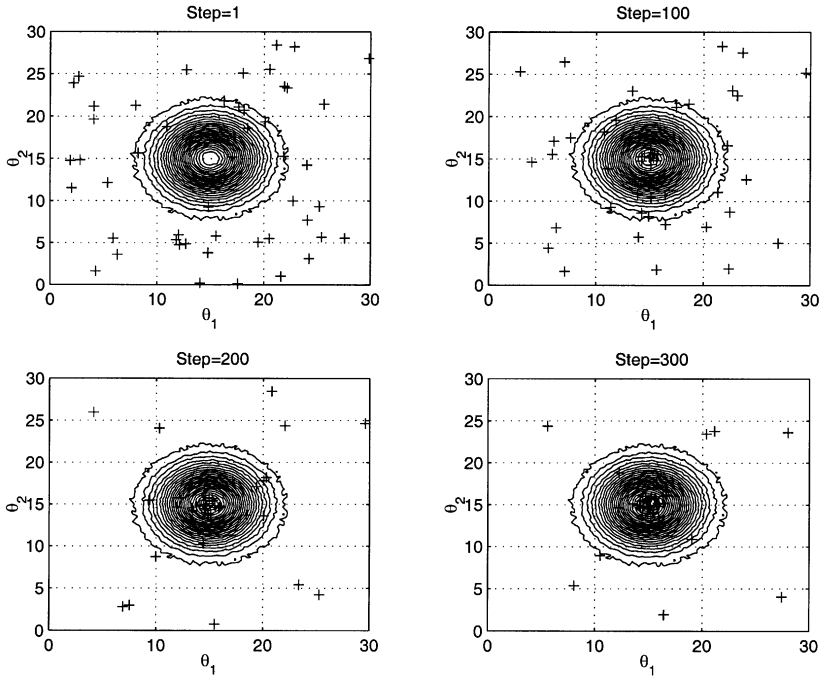

Fig. 2b. Foraging of E. coli in a noisy environment: Bacteria positions at different chemotactic steps (with cell-to-cell attractant).

bacteria fail to find the optimal point even at step 300. Figure 2b demonstrates the results when attractant exists. It is clear that, by performing social foraging, E. coli have better chance in locating the optimal point in a noisy environment, which validates the Grunbaum idea.

3. M. xanthus: Optimization Model and Simulation Results

3.1. Modeling

3.1a. Biology of M. xanthus Social Behavior. Myxococcus xanthus, one type of myxobacterium that lives in soil and on leaves on forest floors, is a gliding bacterium that can move only on solid surfaces (it cannot swim in a liquid medium). When a single bacterium is isolated in an appropriate nutrient-rich environment, it moves forward and backward and it seems to make no progress. In other environments, it will more frequently move in one direction than in the other so there can be net movement. As it moves,

it lays down a slime trail. It seems that the slime may help it to stick to a solid so it can move, and it seems to grease its path to make movements easier. The mechanisms for gliding are not yet well understood. If in its movements the bacterium encounters a trail (perhaps of another bacterium), it will tend to get on that trail, and it tends to move faster on a previously laid trail than when it has to lay its own trail. Hence, when you observe the motile behavior of the bacteria you see that the slime secreted by each bacterium tends to attract other bacteria to follow it. The tendency of one cell to prefer to follow the slime trails by previously passing cells results in one type of mechanism for intercellular cohesion in that it will tend to keep bacteria together since they will tend to follow each other.

This slime-trail following mechanism is not the only means to achieve cell-cell communication in M. xanthus. Complex intercellular chemical signaling in Myxobacteria can cause significant changes in motile behavior and activity of the cells. For instance, under certain conditions, they engage in social foraging (vegetative swarms) where the moving swarm releases complex mixtures of chemicals to help digest nutrients and other species of bacteria that are their prey. Analysis has shown that such group foraging can increase the energy intake per unit time for each cell over the case when a cell forages alone; hence, social foraging provides a selective advantage.

Current evidence seems to indicate that single cells are not chemotactic (see Ref. 36), even though some evidence has suggested that a single cell can avoid repellants and exhibit a type of kinesis; e.g., when a M. xanthus enters a group of E. coli (a prey), it stops moving until all of the E. coli are digested. Instead, some argue that a group-chemotactic mechanism is possible (see review in Refs. 26 and 36). For this, some complex types of signaling may be present where each cell somehow learns something about the quality of life of the other bacteria in the swarm and move in the direction of the one (or the ones) who are doing the best. But the sensing mechanisms are not well understood. One theory could be that, when a cell is finding lots of food, a special chemical is released that every other cell is chemotactic toward. This would tend to pull the cells together into a feeding frenzy that results in even more efficient energy acquisition than if the cell were alone. Now, if a cell is on the edge of the swarm so that, due to chemical diffusion, its attraction to the swarm is lower than for cells in the middle, then it may act to move faster away from the swarm. If the cells always try to stay with their neighbors, then fast moving edges of the swarm could pull the group in different directions (or perhaps a split could occur).

For M. xanthus, when nutrients are in short supply, hundreds of thousands of the cells aggregate into a multicellular structure called a mound, which is a special type of fruiting body. In the formation of the fruiting body, some cells die and others turn into spores (thick-coated spherical cells

resistant to heat, desiccation, and long-term starvation). The M. xanthus fruiting body is visible by the naked eye and can be seen as yellow, red, or green specks on decaying leaves or bark of trees. The entire fruiting body can be picked up by wind, water, or an animal that passes by and can be transported to destinations more suitable for establishing a new colony. Hence, from one perspective, motility may be viewed as being aided by other environmental factors, the ones called elimination and dispersal events earlier.

3.1b. Stochastic Cellular Automaton Model. In our model, both the spatial and temporal domains are discretized with a regular grid. We assume that each bacterium occupies one grid point at any time point and that it moves with a constant speed of one cell per each time step. The spatial domain is a three-dimensional space $\Omega \in R^3$ with a uniform $N_x \times N_y \times N_z$ grid units, where N_x, N_y, N_z are the number of grid partitions in the x, y, z directions, respectively. Ω is a closed space so that no bacteria may escape from it. If a bacterium reaches the boundary of Ω, it either moves along it or back to the interior of Ω, determined by the rules listed below.

At the beginning of our simulation, all bacteria are randomly distributed on the ground of Ω [i.e., on the (x, y) plane]. They keep moving on the ground layer until they begin to form a fruiting body, when they will try to climb onto each other and form a multilayer stack of cells that comprise the fruiting body. Since M. xanthus is a kind of soil bacteria, we assume that nutrients, if any, are available only on the ground.

With time passing by, different bacteria may be in different states. Specifically, depending on which life cycle it is in, a bacterium may secrete different chemicals such as slime, swarming attractant, and fruiting body attractant. It may also change into a spore or die. We list the rules that specify the behaviors of each bacterium as follows:

(B1) Each bacterium moves at a fixed speed, one cell per time step.

(B2) If and only if a bacterium moves along the ground, it does lay down slime. Each deposition amount of slime is fixed and the slime evaporates at a constant rate.

(B3) Each bacterium will secrete swarming attractant only when the average nutrient concentration obtained over the previous m steps is higher than a certain threshold τ_1.

(B4) Each bacterium will secrete fruiting body attractant only when the average nutrient concentration it obtained over the previous m steps is lower than a threshold τ_2, $\tau_2 < \tau_1$.

(B5) To determine its next movement, a bacterium detects its neighboring grid points. The detection continues until the bacterium changes into a spore or dies.

(B6) If a bacterium has secreted a fruiting body attractant for n steps, it either dies or changes into a spore. A dead bacterium is removed from the space. A spore cannot move around, secrete chemoattractant, or lay down slime; it just remains stationary and occupies a space.

(B7) Neither a bacterium nor a spore may float in the air, but one bacterium may climb on top of another. No bacteria or spores may occupy the same grid at the same time point.

To explain these rules in more detail, we define some parameters and variables first. For a simulation with a population of N bacteria and T time steps, we employ the definitions below:

$P(n, t)$, the coordinate of the grid point occupied by the nth bacterium at time step t;

$S_{sa}(n, t)$, the swarming attractant-secreting state of the nth bacterium at time step t, with $n = 1, \ldots, N$, $t = 1, \ldots, T$, and

$$S_{sa}(n, t) = \begin{cases} 1, & \text{if the } n\text{th bacterium is secreting swarming attractant,} \\ 0, & \text{if the } n\text{th bacterium is not secreting swarming attractant.} \end{cases}$$

$S_{fa}(n, t)$, the fruiting-body attractant-secreting state of the nth bacterium at time step t, with $n = 1, \ldots, N$, $t = 1, \ldots, T$, and

$$S_{fa}(n, t) = \begin{cases} 1, & \text{if the } n\text{th bacterium is secreting fruiting body attractant,} \\ 0, & \text{if the } n\text{th bacterium is not secreting fruiting body attractant.} \end{cases}$$

We model the effect of the swarming attractant, fruiting body attractant, and nutrient consumption of bacteria as Gaussian functions with different magnitude and variance. Let $p \in \Omega$ be the 3D coordinate of a gridpoint. We employ the definitions below:

$J_{sa}(p, p_0)$, the attracting effect of a swarming attractant at position p produced by a bacterium at position p_0, with d_{sa} and w_{sa} being the magnitude and diffusion of the swarming attractant, and

$$J_{sa}(p, p_0) = d_{sa} \exp(w_{sa} \|p - p_0\|^2);$$

$J_{fa}(p, p_0)$, the attracting effect of a fruiting body attractant at position p produced by a bacterium at position p_0, with d_{fa} and w_{fa} being the magnitude and diffusion of the fruiting body

attractant and

$$J_{fa}(p, p_0) = d_{fa} \exp(w_{fa}\|p - p_0\|^2);$$

$J_c(p, p_0)$, the amount of nutrient consumed at position p by a bacterium at position p_0 in each bite with

$$J_c(p, p_0) = d_c \exp(w_c\|p - p_0\|^2);$$

$J_{sl}(p, n, t)$, the deposition amount of slime at position p by the nth bacterium at time step t, with the constant λ being the amount of each deposition:

$$J_{sl}(p, n, t) = \begin{cases} \lambda, & \text{if } p = P(n, t), \\ 0, & \text{if } p \neq P(n, t). \end{cases}$$

Then, we have the following consequences:

$$J_{SA}(p, t) = \sum_{n=1}^{N} J_{sa}(p, P(n, t))S_{sa}(n, t),$$

which is the concentration of swarming attractant at position p and time step t;

$$J_{FA}(p, t) = \sum_{n=1}^{N} J_{fa}(p, P(n, t))S_{fa}(n, t),$$

which is the concentration of fruiting body attractant at position p and time step t;

$$J_N(p, t) = J_N(p, t_0) - \sum_{t'=t_0}^{t} \sum_{n=1}^{N} J_c(p, P(n, t')),$$

which is the concentration of nutrient at position p and time step t, with t_0 being the starting time of the simulation;

$$J_{SL}(p, t) = \sum_{t'=t_0}^{t} \sum_{n=1}^{N} \lambda^{t-t'} J_{sl}(p, n, t'),$$

which is the density of the slime trail at position p and time step t;

$$J(p, t) = J_N(p, t) + J_{SL}(p, t) + J_{FA}(p, t) + J_{SA}(p, t),$$

which is the overall cost function at position p and time step t.

The first rule is implemented mainly for simplicity. Time-varying speed could be added easily to the model. Biologically, the bacterium is a rodlike cell, with the ratio of cell width to cell length being around $1/8$. But for the convenience of modeling, we assume that each bacterium takes up only two

neighboring grid points, which indicate its head and tail, respectively, though head or tail does not exist in biological terms (Ref. 14).

When a bacterium is moving along the ground, it deposits a fixed amount of slime on each grid point it passed. It is observed that M. xanthus prefers to move on slime trails. Thus, a bacterium that comes across this slime trail tends to slide onto it and follow it. On the one hand, the slime trail decays as time goes by. On the other hand, it can be accumulated. That is, if several bacteria passed the same grid point, the resultant density of slime trail at that point will simply be the sum of the individual slime trail densities. However, we assume also that the sensing organ of a bacterium becomes saturated at high concentration of slime trails. So, we modify the previous expression for J_{SL} as

$$J_{SL}(p, t) = \min(J_{SL}(p, t), \gamma),$$

where γ is the saturation density of slime trail. This means that a spot with very high slime trail density may have a similar attracting effect to a spot with medium slime trail density.

Besides slime, a bacterium may also secret chemoattractant under certain conditions. When the environment is rich in nutrients, M. xanthus will perform foraging and try to find the place with highest density nutrients. A single bacterium might get trapped in a local extremum if the environment is noisy. But, when many of them work together, they may pull each other into the global extremum (Ref. 4). This is realized by following the slime trails and secreting the swarming attractant. When an environment has limited nutrients, it will be consumed by the bacteria, with the consumption function J_c defined above. Then, more and more bacteria will get starved. In such cases, M. xanthus begins to request the formation of a fruiting body. This is achieved by stopping the secretion of a swarming attractant and starting the secretion of another chemoattractant, the fruiting body attractant. It will keep secreting this attractant until enough nutrient is available again, it changes into a spore, or it dies.

Basically the effect of a fruiting body attractant is quite similar to that of a swarming attractant, i.e., attracting other bacteria to swarm. But the former purpose is to build a fruiting body instead of foraging. Moreover, the two chemoattractants have different diffusion and strength. It is also important to note that, although both slime and chemoattractant are chemicals with attracting effects, they are different in that the chemoattractant diffuses while the slime does not (Ref. 14).

To specify how a bacterium moves at each time step, consider Fig. 3 which shows a three-layer cubic network. The big solid black circle in the figure represents the head of the bacterium and the small solid circle indicates, in this case, where its tail is located. Thus, a bacterium is modeled as

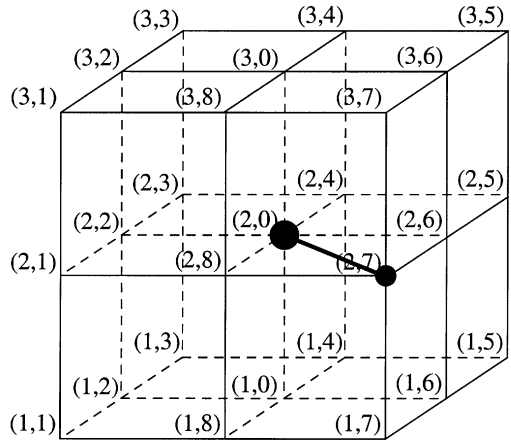

Fig. 3. Illustration of M. xanthus' movement on a cubic network.

occupying two neighboring grid points and it has a specific orientation in terms of the moving direction. Note that, in our model, we assume that only the head position of a bacterium cannot be cooccupied, while the tail position can be. That is, no two bacteria can have their heads at the same position at the same time, but their tails can overlap; also a bacterium's head can occupy another bacterium's tail position. Therefore, the tail is merely used for locating the bacterium's orientation, which is important for determining its movement on the next time step, detailed as follows.

From Fig. 3, we can see that, for a bacterium, there are 26 neighboring points, which are denoted by (i, j), where $i = 1, 2, 3$, and $j = 0, 1, \ldots, 8$, excluding the point (2, 0), which is the current location occupied by the head of the bacterium. To decide which position to move into on the next time step, a bacterium must be able to detect the cost values of some of its neighboring points. Here, we assume that for a bacterium with the same orientation as shown in Fig. 3, it can sense only the neighboring points corresponding to the locations (i', j'), where $i' = 1, 2, 3$ and $j' = 1, \ldots, 5$. The choice of the candidate next-step positions is made intuitively. Other reasonable choice is feasible. From the view of algebra, different neighboring positions have different distances to the bacterium. For example, the distance of (3, 8) to (2, 0) is slightly longer than that of (2, 8) to (2, 0). But this is not regarded as an essential aspect of the problem. Thus, we simply assume that a bacterium needs only one time step to reach any of the neighboring points.

To determine the next step movement, a bacterium simply computes the cost values $J(p, t)$ on these neighboring points and chooses to move to the best one available. Note that the available best cost position may not

always be the best cost position, since the movement of a bacterium cannot violate the rules that we listed previously. One example is that the position may have already been occupied by the head of another bacterium. Another example is that forcefully moving into the best cost position may mean that the bacterium will be floating. Here, by floating we mean a position which has no other bacteria staying at the 3×3 neighboring points underneath. In Fig. 3, we say that the bacterium is floating if there is no bacteria on position $(1, j)$, where $j = 0, 1, \ldots, 8$. Sometimes, it may happen that none of the possible moving positions are available; i.e., they are either floating positions or are occupied by other bacteria. Then, the bacterium will stay at its current spot at that step. But we assume that it will turn around, i.e., change its orientation by moving its tail, hoping that an exit may be found by such efforts. It is also possible that all of the available positions and current spot occupied by the bacterium become floating positions due to the movement of other bacteria. In such a case, the only movement of the bacterium is to drop down due to gravity, so long as it is on a layer other than the ground.

The above description is for the general case. Actually, such three-dimensional search happens only when the bacteria are forming a fruiting body. When the bacteria are foraging, they move only along the ground and perform a two-dimensional search. That is, they detect only the neighboring positions in the same layer. Again, taking the bacterium in Fig. 3 as an example, it will compute only the positions $(2, j)$, $j = 1, \ldots, 5$, when it is foraging. Of course, in this case, the positions $(1, j)$, $j = 0, 1, \ldots, 8$, are meaningless.

During the formation of a fruiting body, some bacteria die and others change into spores gradually. We assume that the probability of death is constant. Dead bacteria are eliminated permanently. Bacteria in spore status will not move around and respond to stimulus like chemical attractants. Their only possible movement is dropping down due to gravity, if they are in layers higher than the ground. Only when the spore touches the ground and gets nutrient again can it recover.

3.2. Simulation Results. In this simulation, we used a noise-contaminated quadratic nutrient profile, which has the best value around the position $(0.75, 0.75)$ on the (x, y) plane. This nutrient profile is used in all of the following simulations except the last one. All the simulations are run in 128 steps.

To demonstrate the effect of social foraging, we run two simulations. In both simulations, there are 30 cells which are randomly distributed on the (x, y) plane initially. Though in reality the number of M. xanthus in a typical social foraging group will be on the order of hundreds of thousands

or millions, we believe these simulations can still illustrate some characteristics of social foraging of M. xanthus. In the first simulation, the bacteria will not secrete any chemicals, which means that they cannot get any help or hint from others and hence have to work independently. Therefore, this shows us the nonsocial foraging effect, which is shown in Fig. 4a. In the second simulation, the bacteria can both secrete the swarming attractant and lay down the slime trails, by which they communicate with each other. Thus, it demonstrates the result of social foraging, which is shown in Fig. 4b. As we expected, in social foraging, most cells succeeded in finding the approximate location with the best nutrient, while those bacteria which foraged independently failed to achieve this.

Obviously, the success of social foraging lies in the communication among bacteria. The communication is realized by secreting and sensing the chemical attractant and the slime trails. Now, we compare via simulation the individual effect of these two components, which cannot be realized in the real world. Again, the bacteria are randomly distributed on the (x, y) plane initially. The final swarming results are shown in Fig. 5. Comparison of Fig. 5a and 5b shows that the simulation with only chemoattractant has a better swarming result.

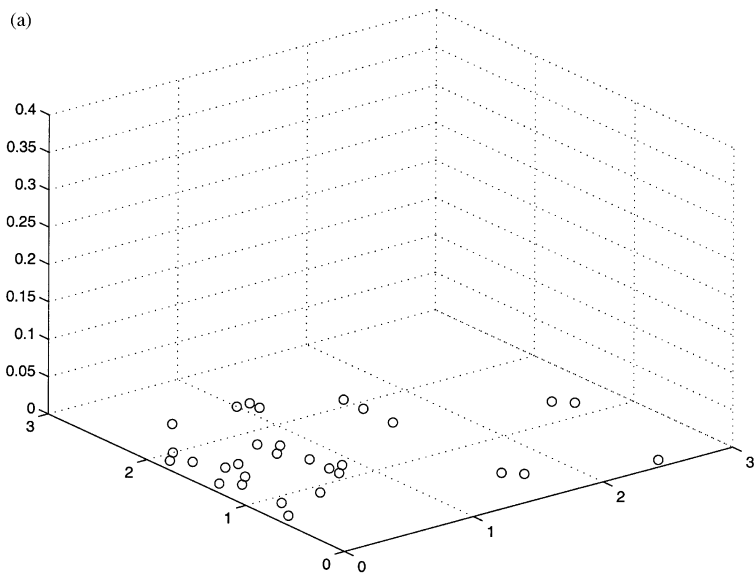

Fig. 4a. Comparison of M. xanthus swarming under different foraging: Final position of M. xanthus without social foraging.

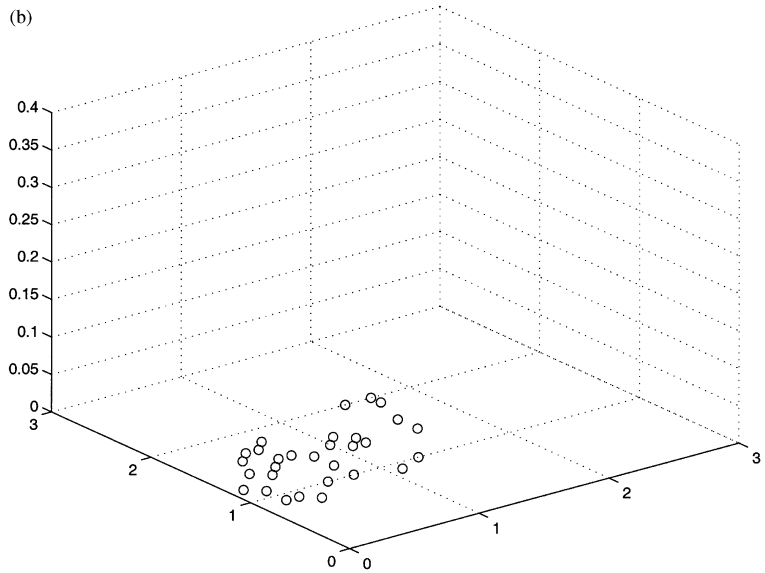

Fig. 4b. Comparison of M. xanthus swarming under different foraging: Final position of M. xanthus with social foraging.

At last, we show the whole life cycle of M. xanthus in one simulation, with the focus on demonstrating the formation of the fruiting body. In this simulation, we increase the number of bacteria to 150 and run 64 time steps. Also, we change the nutrient profile into one which has its highest concentration of nutrients at the center of the plane and is not contaminated by noise. Moreover, we add the nutrient consumption function J_c into this simulation, which we did not do in the previous simulations so that it would not obscure the characteristics that we wanted to illustrate there. By making these modifications, we may not only demonstrate the complete life cycle of the bacteria, but also get a better view of the formation of a fruiting body without being diverted by other less significant aspects in this issue. The simulation results are shown in Fig. 6. All the plots in the figure correspond to a different time step of the simulation. For example, Fig. 6b is for time step 16, and so on.

At the beginning of the simulation (i.e., time step 0), there are nutrients available on the ground and the bacteria are distributed randomly over it. Since the highest concentration of nutrients is located around the center of the plane, those bacteria will be moving toward there. With the time passing by, the nutrient is soon eaten up. Thus, the bacteria get starved and begin to form a fruiting body. They come together and climb up and down each

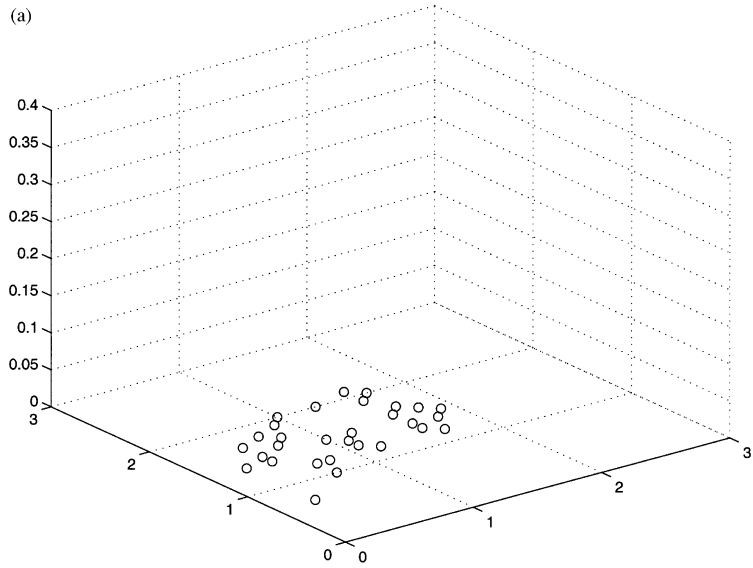

Fig. 5a. Comparison of swarming results under different conditions: Social foraging with attractant only.

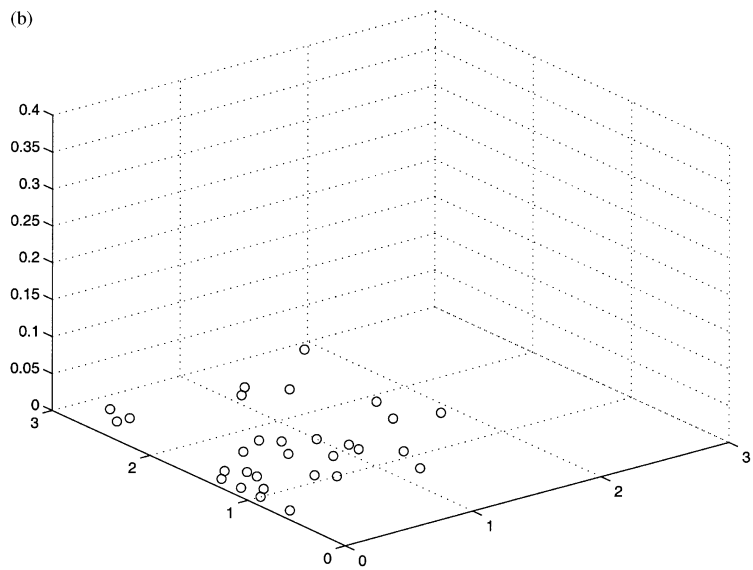

Fig. 5b. Comparison of swarming results under different conditions: Social foraging with slime trails only.

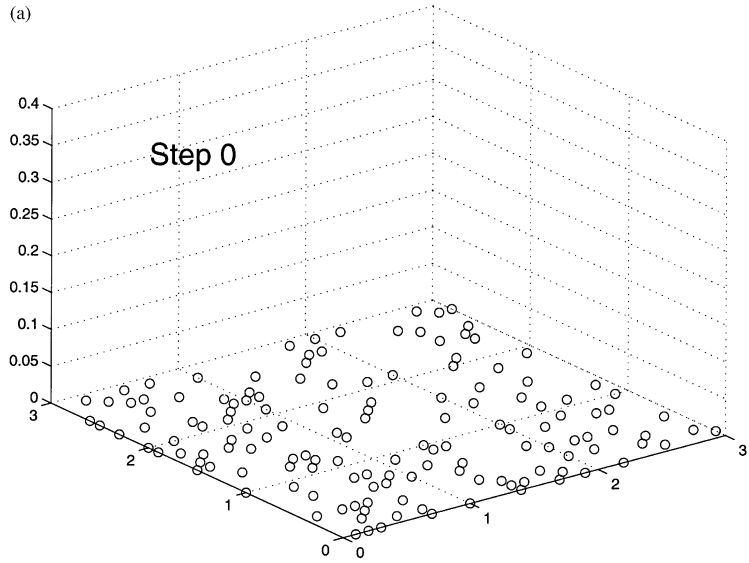

Fig. 6a. Complete life cycle of M. xanthus: Initial status.

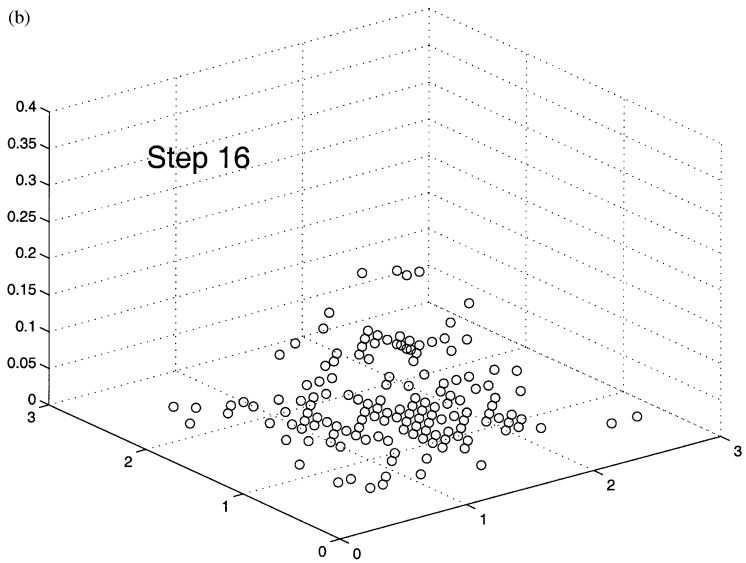

Fig. 6b. Complete life cycle of M. xanthus: Formation of fruiting body.

other, as shown in Fig. 6b. During the formation of the fruiting body, some bacteria change into spores and some die. The fruiting body reaches a certain height(in this case, the maximum number of layers is six during the whole cycle), then its shape does not change much any more, as shown in Fig. 6c. In our simulation, nutrients are made available again in step 44, when the germination process begins. After that, the fruiting body begins to collapse. Figure 6d, which corresponds to step 64, shows again that almost all the bacteria touch the ground, recover from spores, and move around to search for nutrient. The simulations give us some basic ideas about the life cycle of M. xanthus.

From all of the above simulations, we can see that, with social foraging, the bacteria can overcome noisy nutrient environments and pull each other into the most nourishing places, which can be very important in real life since it increases the chance of survival. The simulations capture this important feature. Note that, in Fig. 4b, the bacteria did not really swarm at the position (0.75, 0.75), which is the position with highest concentration of nutrient on the clean nutrient map. This may be due to the fact that the addition of noise changes the apparent best nutrient value, and thus its corresponding position.

But the individual effects of the chemoattractant and slime trails is not quite as convincing since their characteristics have not been studied in recent

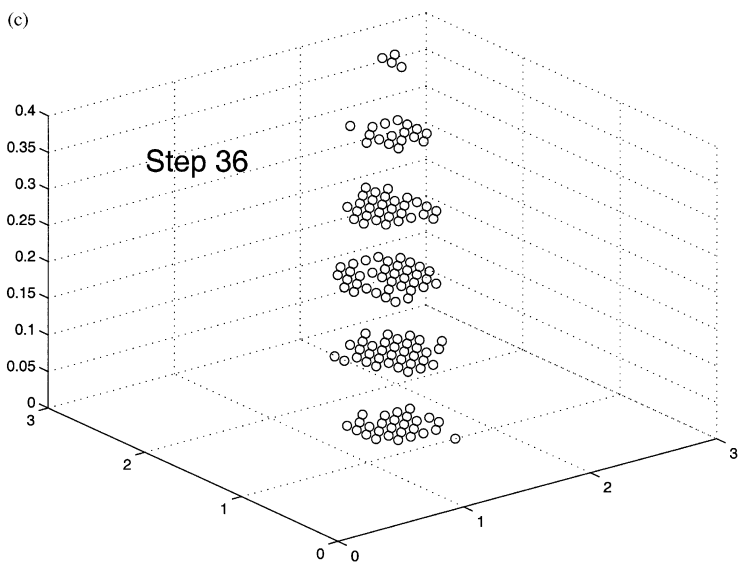

Fig. 6c. Complete life cycle of M. xanthus: Fruiting body formed.

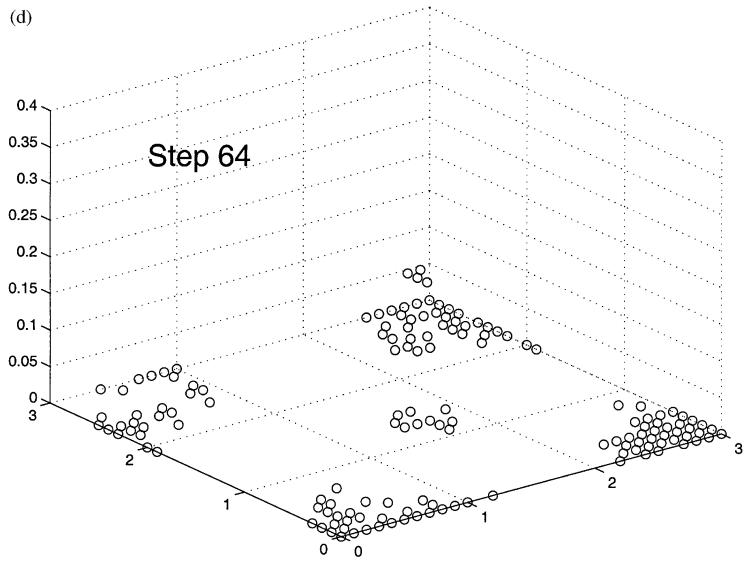

Fig. 6d. Complete life cycle of M. xanthus: Fruiting body collapsed.

papers. Slime trails are readily observable and their effects are significant. But this does not exclude the possibility of the chemoattractant having the same significance, if not more. In the simulation, we assume that the attractant effect is diffusing through the whole nutrient plane, that is, every grid point on the ground of the space Ω. While the effect of the slime trails is assumed to exist only on certain grid points once passed by some bacteria instead of on the whole plane, this assumption may bias the result. Moreover, lacking a relevant biological study, we have to set the attracting magnitude of the attractant and slime trails arbitrarily, which may also contribute to the observed simulation result.

In summary, this model captures some important aspects of M. xanthus' life. It also gives some ideas about which experiments would help us understand the life cycle of M. xanthus.

4. Conclusions

The main conclusions that can be drawn from this study include:

(i) A continuous optimization model is appropriate for E. coli and a stochastic cellular automaton is appropriate for M. xanthus.

(ii) The models of social foraging are also distributed nongradient optimization methods and each has the potential to be useful in practical optimization problems (e.g., engineering design, online distributed optimization in distributed computing and cooperative control).

(iii) Grunbaum's principle of social foraging for the purpose of climbing noisy gradients emerged for two species of bacteria, even when very different modeling/optimization methods were used (i.e., a continuous optimization model and a 3D stochastic cellular automaton).

There are a wide variety of fruitful research directions. There are ways to improve the models (e.g., modeling more dynamics of cell motion). Other species of bacteria could be studied, and indeed it would be interesting to see if Grunbaum's principle works for others species of social foraging animals. Moreover, it remains to be seen how practically useful the optimization algorithms are for engineering optimization problems. Claims of practical utility of any optimization algorithm are difficult to make; they depend on the theoretical properties of the algorithm, theoretical and empirical comparisons to other methods, and extensive evaluation on many benchmark problems and real-world problems.

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