Chaos–order transition in foraging behavior of ants

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The study of the foraging behavior of group animals (especially ants) is of practical ecological importance, but it also contributes to the development of widely applicable optimization problem-solving techniques. Biologists have discovered that single ants exhibit low-dimensional deterministic-chaotic activities. However, the influences of the nest, ants' physical abilities, and ants' knowledge (or experience) on foraging behavior have received relatively little attention in studies of the collective behavior of ants. This paper provides new insights into basic mechanisms of effective foraging for social insects or group animals that have a home. We propose that the whole foraging process of ants is controlled by three successive strategies: hunting, homing, and path building. A mathematical model is developed to study this complex scheme. We show that the transition from chaotic to periodic regimes observed in our model results from an optimization scheme for group animals with a home. According to our investigation, the behavior of such insects is not represented by random but rather deterministic walks (as generated by deterministic dynamical systems, e.g., by maps) in a random environment: the animals use their intelligence and experience to guide them. The more knowledge an ant has, the higher its foraging efficiency is. When young insects join the collective to forage with old and middle-aged ants, it benefits the whole colony in the long run. The resulting strategy can even be optimal.

foraging dynamics | learning process | low-dimensional chaos | mathematical modeling | synchronization

Both experimental data analysis and mathematical modeling on the foraging behavior of group animals (especially ant colonies) have recently captured much attention due to the high level of self-organizing structures that emerge at the collective level (1–5). Random walking is a widely discussed strategy in the research literature on the foraging behavior of group animals (2, 6–8). Some ecologists maintain that especially Lévy flight schemes can appropriately be used to describe the foraging behavior (6, 7). However, some recent studies have raised doubts whether this is a valid conjecture (2, 8, 9). It is even argued that the rules of locomotion for a walker are always consistent with a purely deterministic model, rather than with a stochastic scheme (9, 10).

On the other hand, in the studies on the foraging behavior of animals, the existence of homes has so far received relatively little attention. Here we argue that the existence of a home or nest influences the foraging process to a large extent. Animals are due to return to their homes because of increasing exhaustion of energy. Moreover each foraging process of an animal is also a learning process. With foraging repetition, long-term memory continues to accumulate, an animal's knowledge about the environment of its nest gets richer, and the region that the animal is familiar with continues to enlarge. Moreover, animals' physical ability and knowledge as determined by their age directly influence their foraging strategy. All these factors deserve close attention.

There is already a rich history of research on the foraging behavior of ant colonies (see, e.g., ref. 11). In particular foraging strategies of ants were discussed in the context of solving distributed control and optimization problems. Already 30 y ago, it was proposed that Lévy flights might characterize the behavior of foraging ants (12). In 1990, Deneubourg et al. designed a well-known wide binary bridge experiment which showed that ants could mark the path followed by a trail of pheromone and find an optimal path between the nest and the food source (13). Based on similar experiments, Dorigo and coworkers (3) developed ant colony optimization algorithms which have been used for solving various difficult problems, including combinatorial optimization, object clustering, and routing selection in communication networks. A limited binary bridge experiment was presented to show that ants could even form two lanes to solve traffic flow problems on crowded branches (4).

However, all these experiments were conducted in special man-designed environments, which were not identical to natural ones, so the ants' free crawling was restricted. It was argued that unrestricted foraging ants might not perform Lévy flights. Moreover, through an experimental study on the dynamical behaviors of an isolated ant and a whole ant colony, Cole (14) discovered that the activity of an ant colony exhibited periodic behavior, whereas the behavior of a single ant showed a low-dimensional deterministic chaotic pattern. In 1993, Solé et al. (15) constructed a 1D chaotic map following Cole to describe the foraging process of an isolated ant. Nemes and Roska (16) designed a cellular neural network model to describe the synchronized oscillating pattern of activity as a result of an array of chaotic dynamic elements placed in a regular 2D grid. In 2006, Li and coworkers (17, 18) developed a chaotic ant swarm model building on Cole's research to describe the phenomenon that the chaotic behavior of a single ant contributes to the self-organization behavior of a whole ant colony. These models have explained some relationships between the chaotic (or random) strategy, individual dynamics, and group dynamics. However, these studies ignored the possibility that the ants also use their own experience and intelligence to guide their foraging. Hence, further studies on the influences of physical ability, age, and knowledge on foraging behavior are needed to explain the biological behavior of ants in nature.

Significance

We have studied the foraging behavior of group animals that live in fixed colonies (especially ants) as an important problem in ecology. Building on former findings on deterministic chaotic activities of single ants, we uncovered that the transition from chaotic to periodic regimes results from an optimization scheme of the self-organization of such an animal colony. We found that an effective foraging of ants mainly depends on their nest as well as their physical abilities and knowledge due to experience. As an important outcome, the foraging behavior of ants is not represented by random, but rather by deterministic walks, in a random environment: Ants use their intelligence and experience to navigate.

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The aim of this paper is to provide a novel perspective on mechanisms of effective foraging of ant colonies. We assume that the foraging process of these animals is entirely controlled by three successive strategies: hunting, homing, and path building. A mathematical model is developed to understand the whole foraging process. We discuss the influences of the special region around the nest, the size of the food source, the search range, the limitation of ants' physical ability, and ants' learning process with respect to foraging behavior. Our analysis suggests that group animals that have a home do not perform random walks, but rather deterministic walks in a random environment. They use their knowledge to guide them and their behavior is also influenced by their physical abilities, their age, and the existence of homes.

Foraging Strategies of Ants

To survive, ants need to leave their nest and forage for food. The survival-of-the-fittest mechanism entails that ants do not only find food, but also an optimal path between their nest and the food source (19, 20). This reflects the collective intelligence of the insects. Nest and food source indeed play important roles in ants' foraging behavior. The whole foraging process of ants may be described by three strategies: hunting, homing, and path building.

Hunting Strategy. During the first phase in foraging, some ants of the colony leave the nest to search for food; we call these "scout ants" (21). We assume that there is a food source located in some random environment. We consider the search for food as the search for an unknown point (or region). Thus, initially, no ant knows where the food is or in which direction it should go. In particular, there is no pheromone on the path before the food source is found. From Cole's observational results on the behavior of individual ants, we know that ants search chaotically around their nest and initially have no impacts on their neighbors. For the details of chaotic and self-organizing ant behavior, see *SI Text*.

Suppose that initially n ants go out to look for food. These ants forage in a continuous search space S, often denoted R^l, the l-dimensional continuous space of real numbers, i.e., $S = R^l$. Each ant with a position vector $\vec{s}_i = \vec{Z}_i = (Z_{i1}, \ldots, Z_{il})$ attempts to search for the location $\vec{P}_{food} = (P_{food1}, \ldots, P_{foodl})$ of a food source by minimizing an object function (cost function) $f: S \to R$, where $S = R^l$ and $f \geq 0$, is a map from l dimensions real number to real number, and when $\vec{Z}_i = \vec{P}_{food}$, $f(\vec{Z}_i) = f(\vec{P}_{food}) = 0$. In the search space $S = R^l$, the food possesses a small region (i.e., the neighborhood of the point $\vec{P}_{food}$). The bigger the food is, the larger the region is. The values of the function f corresponding to different points in the neighborhood of the food source have an upper bound $\triangle$, where $\triangle$ is a relatively small positive number. Here, larger $\triangle$ means larger region around the point $\vec{P}_{food}$. So the value of $\triangle$ represents the size of the food source. $f(\vec{Z}_i) < \triangle$ means the point $\vec{Z}_i$ locates in a small neighborhood of the food source, i.e., the ant finds the food.

Fig. 1*A* provides a schematic diagram of ants crawling in the search space where the black solid point represents the nest and the green triangle the nearest food source. When food is scarce, ants need to go out to forage many times because they must return to the nest to access the stored energy supply. We have developed a map of the nest–food source–nest motion against time. This is sketched in Fig. 1*B* where the solid dot again represents the nest and the green triangle the food source. The length of the optimal path from the nest to the food source is denoted by L. In this map, ants forage chaotically, setting out at the origin. If they do not find food, then the curve does not pass through the green triangle. Because n ants conduct concurrent searches, there is likely some ant i that quickly finds the food source (Fig. 1*B*). This hunting strategy, whereby ants leave the nest and return to it, is used throughout the foraging process.

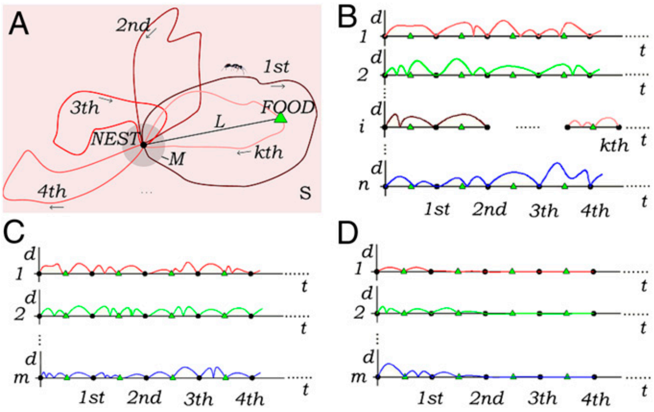

Fig. 1. Stylized presentation of the ant foraging process. The optimized path between the nest (black dot) and the food source (green triangle) has length L. (*A*) Characteristic search behavior of scout ants distinguished by different path colors. S is the overall foraging space and M the nest's neighborhood, which the ants are quite familiar with. (*B*) The foraging motion in S can be mapped onto a simplified trajectory, i.e., a relationship of position vs. time. As detailed in *SI Text*, time t is normalized in a way that highlights periodicity and is represented by the abscissa in *B*–*D*. In the same charts, the ordinate d represents the nearest distance of the respective ant position from the set L. Thus, each foraging excursion appears as a curve segment between two consecutive black dots (home-to-home tour). *B* describes the situation where n scouts search chaotically in parallel. The ith ant happens to find the food source during its kth tour (as indicated by the passing of the trajectory through the green triangle). (*C* and *D*) m-recruited insects are guided by the pheromone traces left by the successful ant i. (*C*) Initially, the pheromone intensity is rather low, thus its guiding influence on the chaotic ant motion is very small. To find the optimal path, the recruited insects pursue various chaotically selected paths around the route marked by the pheromone from the scout ant i. However, all those paths hit the green triangle because the followers "know" the position of the food source from the pioneer. (*D*) With increasing pheromone concentration around the optimal path, the chaotic foraging regime is gradually overcome. Eventually the new regime emerges where all ants pursue L to convey food from source to nest. Thus, all trajectories become straight lines.

Homing Strategy. The existence of a nest has an important influence on the behavior of the ants during the whole search for food. The homing strategy is triggered when a foraging ant makes a decision to return to the nest. The aim of that strategy is to find the home most efficiently. The nest of the ants is denoted by $\vec{P}_{nest} = (P_{nest1}, \ldots, P_{nestl})$. Different ants have different knowledge about the environment of the nest, i.e., each ant considers different domains M_i as nest neighborhoods (22). If ant i moves into its nest neighborhood $M_i = \{\vec{Z}_i : \|\vec{Z}_i - \vec{P}_{nest}\| < c_i\}$, then we assume that it has found the nest (Fig. 1*A*), where the neighborhood range is determined by the positive constant c_i, and a larger c_i indicates that the ant has more knowledge about the nest environment. Obviously, older ants have larger c_i because they have more knowledge about their nest. Foraging can be considered as searching for an unknown point (or small region), whereas searching for the nest is considered as searching for a special region with which an ant is very familiar. In the homing process, the ants use chaos and pheromone in combination with their own knowledge to search for the nest.

Different ants have different search ranges, different continuing search times, and different search paths. The starting time of the homing strategy is very important. If it is triggered very early, then the probability of ants finding food will be minute; if it happens very late, however, then the ants may not be able to return to the nest because their energy is exhausted. That is, each ant has its own searching time threshold, i.e., the tiring time t_{tired}. When t_{tired} is reached, the ant should start its homing strategy, independent of having found food or not.

Path-Building Strategy. When a scout ant finds a food source, it begins returning to the nest and leaving pheromone on its return path as a means of communicating to fellow ants the location of the food and appropriate paths (3, 4). Once the scout ant has returned to the nest, it will gather recruited ants to follow its path marked with pheromone. We assume there are m recruits. In addition, there are still some freely walking scout ants looking for food in the search space.

Both the chaotic walking and the pheromone have important impacts on the foraging process of recruited ants. Pheromone influences their choice of path making. Ants encountering a path previously laid with heavy amounts of pheromone are more likely to decide to follow it. Pheromone is an evaporative substance, though. An autocatalytic collective behavior of recruited ants emerges, where the shorter the path, the higher its pheromone density becomes (23). During the initial construction phase of the optimal path, the orchestration between ants is weak, and chaotic movement dominates their behavior because of the very low density of pheromone. Fig. 1*C* depicts the initial foraging behavior of m recruited ants. This figure illustrates how the ants initially foraged chaotically around the route marked by the pheromone of the scout ant, while leaving more pheromone on their wandering paths. This means that chaotic walking and pheromone interact in the optimization process.

We use the pheromone field concept to help us understand the behavior of the recruited ants. The pheromone field is the cause of self-organization among ants and is used to direct their movements. As time passes, the pheromone left by the recruited ants on their paths increases gradually, and a distinct pheromone field is constructed between the food source and the nest. The reinforcement of pheromone continues to weaken the chaotic behavior of the ants. The evaporation of the pheromone causes the density of pheromone on the shorter path to increase more quickly than on the longer one, which in turn causes more ants to choose the shorter path. The increment of pheromone density on the paths is equivalent to a decrement in the chaotic crawling of insects (*SI Text*). During the formation of the pheromone field and the finding of the optimal route, the ants still possess some chaotic crawling, which is eventually superseded by the pheromone signals.

Fig. 1*D* shows the final foraging phase of the m recruited ants. The ants gradually enter a state of ordered periodic motion through self-organization in the colony. Obviously, the chaotic behavior causes the ants to conduct a global search, whereas the pheromone field causes the ants to conduct a local search until they finally converge to periodic movements. In this process, the transformation of dynamical behavior of an ant colony causes the emergence of something that may be called "swarm intelligence."

Thus, we consider the process by which ants begin their foraging and form their optimal path to be an intelligent process, whereby the status of ants is transformed from an asynchronous chaotic regime into a collective synchronous periodic act. Ants use their intelligence and experience to guide their foraging process. We regard a foraging cycle of ants as the process in which ants leave their nest to find a food source until an optimal path is found and then convey all of the food to their nest. After one foraging cycle is completed, the ants initiate another one to survive, searching for a new food source.

Results

Now we show how the basic principles sketched above are applied. For simplicity, we assume that there is only one food source in the search space and that there is only one optimal route between the food source and the nest. The chaotic model $Z'(t+1)=Z'(t)e^{\mu(1-Z'(t))}$, constructed in ref. 15, is introduced to mimic the random activity of a single ant at the beginning of the foraging process, where $Z' \in R^{+}$ is a continuous variable and μ a positive constant. When $\mu=3$, the system is in a chaotic state (15, 18).

Next, we take into account the influence of the nest and the food source on the ants' motion. Here, the organization of ants sets in under the competing influences of the pheromone and the ants' chaotic crawling. The characteristic variable of chaotic crawling represented by $y_i(t)$ is introduced, where $0 \le y_i(t) < 1$, and the value indicates the degree of chaotic crawling. A larger y means a higher degree of chaotic crawling. Based on the mechanism of chaotic annealing (24), the continual decrement dynamics of $y_i(t)$ is represented by $y_i(t)=y_i(t-1)^{(1+r_i)}$, which depends on the self-organization factor r_i (see *Methods* for details on r_i). The movement adjustment of each ant is executed as follows:

$$\begin{aligned} Z_{ik}(t+1) = {} & \left(Z_{ik}(t)+V_k\right)e^{\left(1-e^{-ay_i(t)}\right)\left(3-\psi_k\left(Z_{ik}(t)+V_k\right)\right)} \\ & -V_k+e^{-2ay_i(t)+b}\left(\left|\sin(\omega t)\right|\left(P_{foodk}-P_{nestk}\right)-\left(Z_{ik}(t)-P_{nestk}\right)\right), \end{aligned} \quad [1]$$

where ψ_k can adjust the search range, V determines the search region of ant i and accounts for the option that ants can roam diverse realms, ω is used to adjust the frequency of ants' periodic oscillation between the nest and the food source, a is a sufficiently large positive constant such that the variable $y_i(t)$ could have a large enough impact on the position vector Z_{ik}, and b is the local search factor which controls the local optimal path strategy. When y_i approaches 0, b begins to work, where $0 \le b < \ln(2)$. If $b \ge \ln(2)$, the system is unstable. When $b = 0$, the system is in a periodic oscillatory regime between the nest and the food source without undergoing the process of a local search. When $0 < b < \ln(2)$, the system starts from a transient chaos state and finally converges to a periodic behavior.

Now we analyze and examine the nonlinear dynamics of the proposed chaotic ant foraging model. We use it to solve a concrete optimization problem whose objective function is defined by $f(x_1,x_2)=(x-0.7)^2\times(0.1+(0.6+x_2)^2)+(x_2-0.5)^2\times(0.15+(0.4+x_1)^2)$, where (0.7,0.5) is the global minimum of the energy function f. To simulate the foraging cycle, we assume that the point (0.7,0.5) is the position of the food source, and (0.4,0.4) is the position of the nest. All of the figures in this section are the results of numerical simulations for Eq. **1**.

Food Hunting and Homing Processes. Ants of different ages have different physical abilities and different knowledge about their nest. The age of the ants thus has a significant impact on their foraging behavior. Fig. S1 displays the foraging probability curves of ants with different ages as △ changes, where △ is the size of food source. We find that when △ is fixed, old and middle-aged ants hit the food source much more easily than the young ones. From Fig. S1, we also see that on the whole, the probability of finding food for an ant increases as △ increases, which is not very surprising.

Obviously, the tiring time t_{tired} and the nest neighborhood range constant c play crucial roles in the search process, which shows that the physical ability and the knowledge the ants have have an important impact on their foraging behavior. Fig. 2 *A* and *B* shows the influence of t_{tired} on the probability an ant finding food for different △. We see first that for a given group size, the foraging success increases as t_{tired} grows. The greater the physical ability of an ant, the larger its t_{tired}, i.e., the greater the physical ability, the easier the foraging. Second, the higher the number of foraging ants, the larger the probability of finding food. This agrees with traditional views reported in existing studies on optimization (3, 17). Third, when the value of t_{tired} is fixed, the larger the size of the food source, the greater the probability of finding food.

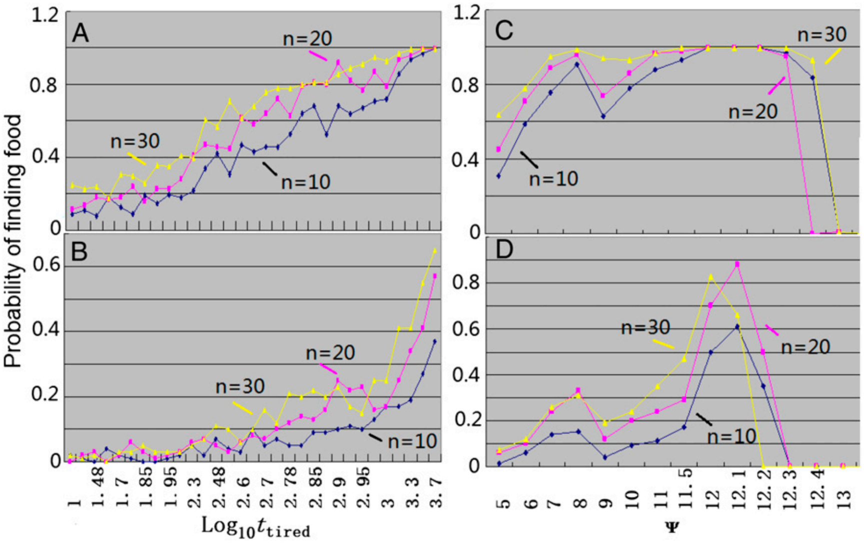

Fig. 2. (*A* and *B*) Influence of the tiring time t_{tired} on different numbers of middle-aged ants finding food, where $c = 0.1$ and $\psi = 7$ and (*A*) $\Delta = 10^{-4}$ and (*B*) $\Delta = 10^{-5}$. (*C* and *D*) Influence of ψ on the probability of finding food for middle-aged ants of different numbers, where (*C*) $\Delta = 10^{-4}$ and (*D*) $\Delta = 10^{-5}$. Different color curves denote foraging ants with different numbers.

The search range has an important influence on the probability of finding food. We show that the increment of foraging probability for the ants is related to the increment of ψ in a nonlinear way. Fig. 2 *C* and *D* depicts the influence of ψ on the probability of an ant finding food. From Fig. 2 *C* and *D*, we conclude first that the larger the value of ψ, the smaller the foraging range—when ψ is very large (e.g., $\psi \geq 13$), the search range is so small that the food source is outside, and the probability of finding food is negligible. Second, when ψ is very small (for example, $\psi = 5$), the probability of finding food is small because the foraging range is rather large. Third, when ψ is within an optimal range (for example, $5 \leq \psi \leq 12$), the probability of finding food initially increases, then decreases and finally increases gain with varying ψ; that is, an optimal choice of the search space is needed for the ants to forage effectively.

Fig. 3 shows the influence of c on the average time of finding food for middle-aged ants with different ψ, where $t_{tired} = 1{,}000$ and $\triangle = 10^{-4}$. The results of Fig. 3 are averaged over 100 cycles. As seen from Fig. 3, we conclude first that the larger the value of c, the smaller the average foraging time and the smaller the average homing time. A larger value of the neighborhood range constant c indicates that the ant has more knowledge about the nest environment, which helps the whole ant colony find the food faster. Second, the larger the value of c, the smaller the ratio between average homing time and average foraging time; i.e., the average homing time decreases with increasing knowledge, which helps to raise the foraging efficiency of the ants. This is indeed an appropriate optimization strategy for animals with a home, whereas for other animals other optimization strategies are more appropriate.

To summarize, we find that the physical ability and the knowledge about the environment of the nest strongly influence the foraging behavior of ants. We define an integrated search ability $\Gamma(\mathrm{age}) = (1-\lambda)t_{tired}(\mathrm{age}) + \lambda c(\mathrm{age})$ to represent the synthesized capability of ants searching for food and nest, where "age" evidently denotes the age and λ is a scale factor which determines the proportion of t_{tired} and c in Γ, where $0 \leq \lambda \leq 1$. Thus, we derive a critical value Γ': When $\Gamma > \Gamma'$, an ant is suitable to forage over long distances. Specifically, we obtain an age range in which ants are suitable to search over long distances. Middle-aged ants have a greater physical ability than young and old ones. However, with increasing age, ants have more knowledge of the nest, and the familiar neighborhood range c of a nest increases, i.e., old ants are very familiar with the environment around the nest. Thus, middle-aged and old ants have greater Γ than young ants, so they are suitable to forage over long distances. As for young ants, their foraging success is relatively small. Their main objective is not to find food but to learn, and the learning process is important for the long-term foraging ability of the whole colony.

Finding the Optimal Path. When a scout ant finds a food source, it returns to the nest and gathers the recruited ants to find an optimal path between the food source and the nest. Fig. 4 *A–D* describes the discovery of the optimal path as time passes. Fig. 4

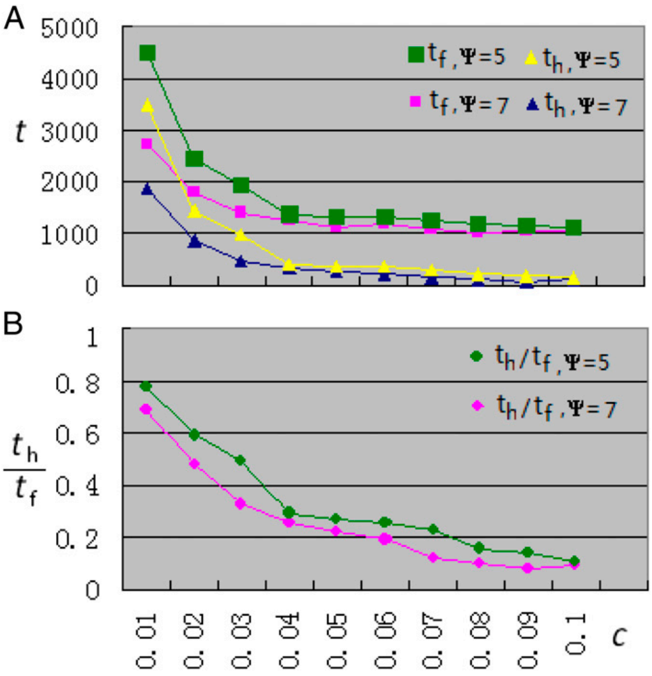

Fig. 3. The influence of c on the foraging behavior of middle-aged ants with different ψ. (*A*) Green and magenta curves show the average times t_f that ants need in one foraging process when $\psi = 5$ and $\psi = 7$, respectively. The yellow and blue curves show the average times t_h at which ants start to use the homing strategy to return to the nest when $\psi = 5$ and $\psi = 7$, respectively. (*B*) The percentages of t_h and t_f. The green curve represents the percentage t_h/t_f when $\psi = 5$ and the magenta line represents the ratio t_h/t_f when $\psi = 7$.

E and F shows the evolution of the variables $y(t)$ and $\|\vec{Z}(t)\|$. We see that the ant colony passes from an initially unsynchronized transient chaotic state into a synchronized periodic state under the influence of the variable $y(t)$. We also see from Fig. 4*E* that $y(t)$ determines the length of the chaotic search. The impact of the pheromone on the foraging behavior of ants is represented by a decrement in the variable $y(t)$. With a continuous decrease of the variable $y(t)$ with time, the influence of the collective on the behavior of an individual ant becomes stronger. When the effect of the social organization is sufficiently large, the chaotic behavior of the individual ant disappears. From Fig. 4*F* we find that the construction of the optimal path for the whole ant colony is similar to that of chaotic annealing, which is an effective optimization mechanism (24, 25). Fig. S2 shows the evolution of $\|\vec{Z}(t)\|$ for different ω. From Fig. S2, we infer that the value of ω has a strong impact on the periodic behavior of the whole ant colony, i.e., the larger the value of ω, the faster the periodic oscillation (or the speed at which ants convey food).

Now we consider the influence of different local search factors b. Here all of the ants have the parameters $r_i = 0.2$ and $\omega = 0.1$. Fig. S3 shows the convergence of the angle ϕ, where $\phi = \left| ((\vec{Z}_i - \vec{P}_{nest})^T (\vec{P}_{food} - \vec{P}_{nest})) / (\|(\vec{Z}_i - \vec{P}_{nest})\| \|(\vec{P}_{food} - \vec{P}_{nest})\|) \right|$ represents the angle between the system's evolution vector $\vec{Z}_i - \vec{P}_{nest}$ and the vector $\vec{P}_{food} - \vec{P}_{nest}$. It shows first that when $b = \ln(2)$, the angle ϕ cannot converge, implying that the foraging process is unstable. Second, when $b < \ln(2)$, the angle ϕ converges to 1 which implies that the ants start from a transient chaotic state and finally converge to a periodic behavior, and they walk directly between the nest and the food source. Third, the closer to ln(2) the value of b, the longer the transient process. And the closer b is to 0, the faster the convergence speed of a local search.

In the above, we make the important assumption that there is only one food source in the search space. Additionally, when two food sources exist with a symmetrical setup, symmetry breaking is more likely to occur. In this condition, the positive feedback drives the transition from the chaotic to the periodic foraging (*SI Text*).

Discussion

We emphasize the generic character of our analysis because a homing strategy in foraging is used by other animals with fixed basis, such as bumblebees, albatrosses, etc. Our model is readily applicable to these situations. For instance, in the foraging process of albatrosses, an optimal fish-searching strategy will not be optimal for home searching. Therefore, if the entire foraging process is assessed, the birds' knowledge about the environment of their home should also be considered. However, this important aspect has received little attention in the existing studies. A homing strategy is not limited to the foraging process of animals, but is also relevant to many aspects of human behavior such as the daily return from work (trivial) and the recurrent accessing of the Internet (less trivial). The impact of human homing behavior on Internet use could be studied, for example, by analyzing how individuals search and roam in cyberspace around their home page.

Learning processes are evidently important for the lives of humans and animals. As demonstrated above, the multitime learning process of young animals benefits the sustainability of the whole group. Continuous learning about changes to the environment is also necessary for the group's adaptation. Storms and heavy wind, for instance, might change the environment with which an animal is familiar. For humans, knowledge that has been proven to be useful has an important influence on behavioral patterns. Young individuals carry on learning about the environment in which they live for several years or even decades. This ability is the basis on which humans have evolved and developed. The views about learning processes expressed in this paper represent a significant departure from current notions about animals foraging strategies, which use either probabilistic distribution schemes or deterministic models. Our findings provide a new perspective on the behavior patterns of certain animals, and of humans, which is of importance in areas as diverse as the spread of diseases, the formation of groups (or networks), the patterns of many social activities, and the evolution of short message (or Web) services.

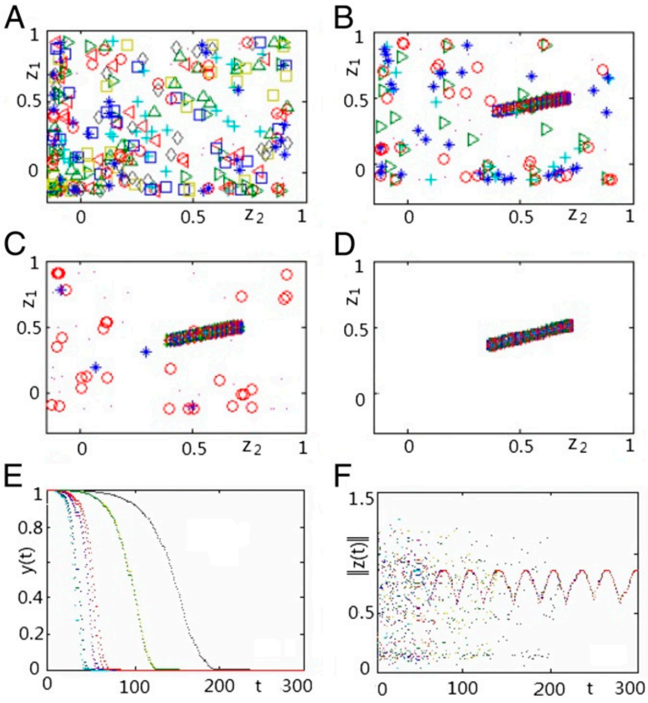

Fig. 4. The evolution of the different variables. (*A*–*D*) Finding the optimal path as time passes, where the point (0.4,0.4) is the position of the nest, point (0.7,0.5) is the position of the food source, and different symbols with different colors represent different ants. (*E* and *F*) The evolution of the variables $y(t)$ and $\|\vec{Z}(t)\| = \sqrt{Z_1^2(t) + Z_2^2(t)}$, respectively, where different colors refer to different ants.

Conclusion

We have developed a model which can be used to explain not only how a single ant uses chaotic behavior to find a food source and its nest in the hunting and homing processes, but also describes how an ant colony organizes itself to find the optimal path between a food source and the nest. Here the transition of ant foraging from chaotic to periodic regimes is explained as a three-stage process. (*i*) An uncoordinated search occurs, which is characterized by the chaotic wandering of scout ants. When a scout finds a food source, it will return to the nest and recruit ants to find the optimal path between the nest and the food source. (*ii*) A cooperative search occurs, which is characterized by a phase during which the recruited ants find the optimal path under the combined influences of chaotic walking and pheromone detection. Individual ants, while still moving chaotically, often deposit pheromone as a form of indirect communication to help other ants find the food source. The collective organization power of the ants increases and their chaotic crawling decreases with the accumulation of pheromone on the paths. This phase lasts until the individual behavior is superseded. (*iii*) Finally, a synchronized periodic motion sets in. All recruited ants are busy conveying the food back and forth along the optimal path between the nest and the food source. In our model, the transition from chaotic to synchronized regimes results from solving an optimization problem (see Table S1). Moreover, according to our analysis, physical ability, experience, and the existence of a nest have important impacts on the foraging behavior of ant colonies.

Through numerical experiments, we reach the following main conclusions. (*i*) The age of the ants is crucial. Old and middle-aged ants find a food source much more easily than the young ones. However, pursuing a strategy whereby young ants forage together with old and middle-aged ants can be optimal because it benefits the long-term foraging prospects of the whole colony. (*ii*) The physical ability of a single ant is also crucial. The greater the physical performance, the better the foraging. Therefore, it is easier for a middle-aged ant to find a food source than younger and older ants. (*iii*) The search range has an important influence on the probability of finding food. In order for ants to forage effectively, the range of the search space should lie within an optimal realm. (*iv*) The foraging efficiency of group animals with homes is clearly different from those without. For group animals, more knowledge about the neighborhood of the nest increases foraging efficiency, i.e., the more knowledge of its home an animal has, the shorter its homing time. Based on these insights, we suggest that for group animals that have a home, their foraging behavior should not be characterized by random walking but rather by deterministic walking in random environments.

Methods

In the foraging process, the movement strategy of a single ant i depends on the current position of the ant $\vec{Z}_i(t)$, the best position found by itself or any one of its neighbors, the position of the nest $\vec{P}_{nest}$, the position of the food source $\vec{P}_{food}$, the characteristic variable of chaotic crawling $y_i(t)$, and the self-organization factor r_i. Generally, the following function is used to describe the whole foraging process of ants:

$$\vec{Z}_i\left(t+1\right)=g\left(\vec{Z}_i(t),\vec{P}_{food},\vec{P}_{nest},y_i(t),r_i\right), \qquad [2]$$

where t means the current time step and g is a nonlinear function.

To mimic an initially chaotic search, we introduce the chaotic model $Z'(t+1)=Z'(t)e^{\mu(1-Z'(t))}$ described by Solé et al. in ref. 15. Let $Z'=(1/\mu)\psi Z$, then we get $Z(t+1)=Z(t)e^{\mu-\psi\cdot Z(t)}$, and the search center is approximately $7.5/(2\psi)$.

Here, the organization of ants sets in under the influences of the pheromone and the chaotic crawling of ants. As time evolves, the pheromone intensity increases and the chaotic crawling of ants is gradually reduced. Based on the annealing mechanism (24, 25), the adjustment of the chaotic behavior of individual ant i is achieved by introducing a successively decreasing dynamical equation represented by $y_i(t)=y_i(t-1)^{(1+r_i)}$. The self-organization factor r_i is used to control the time of the chaotic search. If r_i is very large, the chaotic search is short, and vice versa. Because small changes are desired as time evolves, r_i is chosen typically in the range [0,0.5].

Moreover, the term $|\sin(\omega t)|(P_{foodk}-P_{nestk})-(Z_{ik}(t)-P_{nestk})$ is introduced to achieve periodic oscillating behavior of an individual ant between the nest and the food source, where k is the kth dimension of the position vector. The length of the optimal path is $L=\sqrt{\sum_{k=1}^{l}\left(P_{foodk}-P_{nestk}\right)^2}$. Adjustment of the position of each ant obeys Eq. **1**.

In the food searching process, because there is no organization initially, the position of the food source could be found by setting $r_i=0$. The foraging strategy of ants is to search $\vec{Z}_i$ such that $f(\vec{Z}_i)<\Delta$. When $r_i=0$, $e^{-ay_i(t)}$, and $e^{-2ay_i(t)+b_i}$ approximate to 0, and Eq. **1** applies, we get the following chaotic model:

$$Z_{ik}\left(t+1\right)=\left(Z_{ik}(t)+V_k\right)e^{\left(3-\psi_k\left(Z_{ik}(t)+V_k\right)\right)}-V_k. \qquad [3]$$

That is, the ants walk chaotically throughout the foraging process. Here, $V_k=7.5/(2\psi_k)-P_{nestk}$. The ants center around the nest and search for food. The search diameter ϕ_k depends on ψ_k and $\phi_k\approx 7.5/\psi_k$. Because all the n ants conduct a parallel search in the search space, the ant colony quickly finds the food source $\vec{P}_{food}$.

In searching for the nest, the main aim of ant i is to use its homing strategy to find the neighborhood of its nest such that $M_i=\left\{\vec{Z}_i : \left\|\vec{Z}_i-\vec{P}_{nest}\right\|<c_i\right\}$. Here, older ants have larger c_i because they have more knowledge about their nest.

During the optimal path finding process, self-organization in the ant colony gradually occurs, where $r_i>0$. Under the influence of self-organization, the variable $y_i(t)$ of ants is gradually attenuated to 0. Eq. **1** is then a transient chaotic convergence process. The larger r_i, the faster the alteration of $y_i(t)$, and the faster the self-organization process of the system is formed. When $y_i(t)$ approaches 0, both $e^{-ay_i(t)}$ and $e^{-2ay_i(t)}$ approach 1, and parameter b begins to work. Here, the search model becomes

$$Z_{ik}\left(t+1\right)=Z_{ik}(t)+e^b\left(|\sin(\omega t)|(P_{foodk}-P_{nestk})-(Z_{ik}(t)-P_{nestk})\right).$$

When $0<b<\ln(2)$, the system starts from a transient chaos state and finally converges to a periodic behavior, and the ants walk between the nest and the food source to convey food. That is, the angle ϕ converges from $\phi<1$ to $\phi=1$, where $i=1,\ldots,n$.

Because the chaotic search belongs to a global search and the search caused by pheromone belongs to a local one, the self-organization process is the one that transfers from the global search to the local one. In this process, the ants finally find the optimal path along which they carry the food periodically.

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