Pattern Formation and Optimization in Army Ant Raids

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Abstract Army ant colonies display complex foraging raid patterns involving thousands of individuals communicating through chemical trails. In this article we explore, by means of a simple search algorithm, the properties of these trails in order to test the hypothesis that their structure reflects an optimized mechanism for exploring and exploiting food resources. The raid patterns of three army ant species, *Eciton hamatum*, *Eciton burchelli*, and *Eciton rapax*, are analyzed. The respective diets of these species involve large but rare, small but common, and a combination of large but rare and small but common food sources. Using a model proposed by Deneubourg et al. [4], we simulate the formation of raid patterns in response to different food distributions. Our results indicate that the empirically observed raid patterns maximize return on investment, that is, the amount of food brought back to the nest per unit of energy expended, for each of the diets. Moreover, the values of the parameters that characterize the three optimal pattern-generating mechanisms are strikingly similar. Therefore the same behavioral rules at the individual level can produce optimal colony-level patterns. The evolutionary implications of these findings are discussed.

Keywords
self-organization, army ants, pattern formation, optimization

1 Introduction

Swarm raid patterns in army ants are among the most astonishing social behaviors one can observe in nature. In a matter of hours, thousands of ants leave their bivouac, forming large columns or swarms, with the sole purpose of finding food for the colony. These raids are able to sweep out an area of 1,000 m^2 in a single day. The "Huns and Tartars of the insect world" (Wheeler, cited in [6], p. 573) are a beautiful example of decentralized control and self-organized behavior [1, 11]. The term "army ant" (a.k.a. "legionary ants") refers essentially to the subfamilies *Ecitoninae* and *Dorylinae*, although behavior patterns characteristic of those mentioned above are also found in the subfamilies *Leptanillinae*, *Ponerinae*, and *Myrmicinae* [6]. Such large-scale predatory patterns have been the subject of research by naturalists and myrmecologists for the last century: the structure of the patterns, the relation between division of labor and the raid patterns, their adaptive significance, and so forth. A sample of the reasons for the scientific interest in raid patterns can be found in [6, Chap. 16].

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Different species of army ants display different raiding patterns. The column raiding of *E. hamatum*, the swarm raiding of *E. burchelli*, and the intermediate pattern—between columns and swarms—characteristic of the monomorphic species *E. rapax* would be good examples of the diversity in raid-pattern structure [2]. This diversity was explained by a theoretical model (detailed in Section 2 [3, 4]) that predicted that different patterns were the result of different food distributions and parameter combinations (according to prey preferences), though the underlying mechanism to build raid patterns was the same in all cases. These predictions were successfully tested by means of experiments with *E. burchelli*, whose characteristic swarming pattern changed, when prey distribution was modified, to look like the raiding pattern of *E. rapax* [5].

The mechanism behind raid patterns is a behavioral trait of army ants that has been subject to the forces of natural selection and, as such, it is "partially adaptive and partially an epiphenomenon created by stronger selection occuring on other traits" [9, p. 314]. The question we explore in this article is about the "solution" found by the evolutionary process, that is, did selective forces optimize—in any well-defined sense—those patterns? Since we have a good, tested model of that mechanism, we will use it to look for answers to this question. In what sense are raid patterns optimal? We have chosen the quite reasonable measure of maximizing the food input while minimizing energy expenditure. This will be detailed in Section 4, after a brief review of the search method in Section 3. Finally, a discussion of the biological implications of our results will be provided in Section 5.

2 Army Ant Raid Model

Following previous work by Deneubourg et al. [4], we consider a simple model of army ant raid patterns that involves individual, identical, discrete units moving on a two-dimensional discrete lattice where a pheromone field is created and maintained by the mobile units. More precisely, let $S_k(t)$ be the state of a given ant that will be either $S_k = 1$ or $S_k = 2$ if the ant is searching and moving away from the bivouac or returning back, respectively. Let $\phi(i, j) \geq 0$ be the trail concentration at lattice site (i, j). When ants are searching, they leave one unit of pheromone, unless the total amount of pheromone already exceeds a threshold value σ_1. When returning from exploration with a food item (returning ants always carry a food item) they leave q units of pheromone; now the threshold is σ_2. The pheromone evaporates at a given decay rate δ: At each discrete time step $\phi(i, j) \to (1 - \delta)\phi(i, j)$. Movement involves two different rules, following Deneubourg et al. [4]. These are

1. Probability of movement. A given ant located at (i, j) will move with a probability P_{m} by depending on the pheromone field in the three grid points in front of (i, j) (see Figure 1). If the ant is leaving the nest, it reads

$$P_{\mathrm{m}} = \frac{1}{2}\left[1 + \tanh\left(\frac{\phi(i+1, j+1) + \phi(i, j+1) + \phi(i-1, j+1)}{\phi^*} - 1\right)\right] \tag{1}$$

   (and similarly for returning ants but replacing $i + 1$ by $i - 1$). The parameter ϕ^* represents the concentration of trail pheromone for which the probability of moving per step is 0.5. Here we take $\phi^* = 100$ (changes in this parameter only shift the observed optimal solutions in parameter space but not the obtained patterns). For a justification of the use of the sigmoidal $\tanh(x)$ function, see [4].

2. Once movement is allowed to occur, we have to choose one of the new grid nodes. The nodes with higher pheromone levels are more likely to be chosen. We

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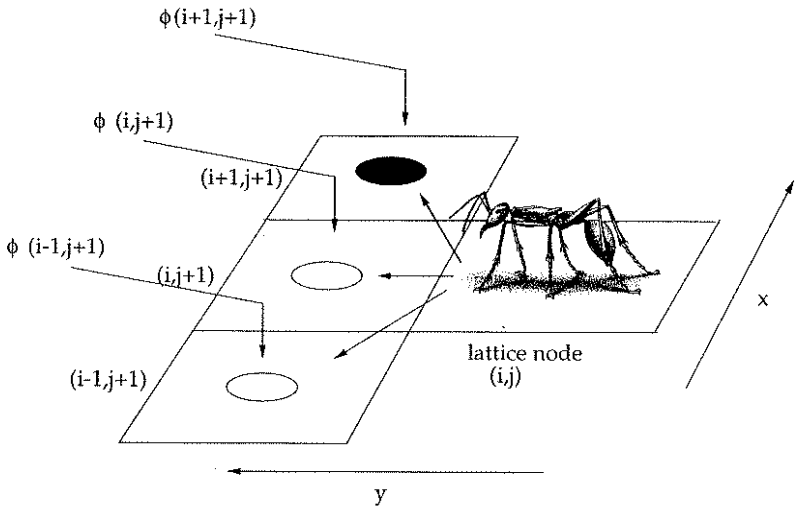


Figure 1. The movement of individual ants will depend on the amount of pheromone lying in the three neighboring sites in front of its current position (see text).

have three probabilities π_L, π_0, and π_R indicating left, central, and right front nodes, respectively. These probabilities are

$$\pi_{\mathrm{L}} = \frac{1}{C}[\mu + \phi(i-1, j+1)]^2 \tag{2}$$

$$\pi_{\mathrm{R}} = \frac{1}{C}[\mu + \phi(i+1, j+1)]^2 \tag{3}$$

and obviously $\pi_L = 1 - \pi_R - \pi_0$. Here C is given by

$$C = [\mu + \phi(i+1, j+1)]^2 + [\mu + \phi(i, j+1)]^2 + [\mu + \phi(i-1, j+1)]^2$$

This choice of a sigmoidal-like function is based on experiments [5]. The parameter μ weights the attractiveness of empty nodes. If the chosen node is such that the total number of ants exceeds a maximum value A_{m}, then no movement is allowed to occur (here we use $A_{\mathrm{m}} = 30$). Two additional rules are required: (a) lost ants (i.e., those that reach the limits of the lattice) are removed from the system; (b) new ants enter from the bivouac, here located at $(1, L/2)$. This is a fixed number (here we use $N_{\mathrm{b}} = 10$) but if the bivouac site is already at the limit A_{m}, no new ants are added. Other choices of the nonlinear (sigmoidal) function have been tested, for example,

$$\pi_{\mathrm{R}} = \frac{1}{C}\left[\phi(i+1, j+1)^2/(\theta^2 + \phi(i+1, j+1)^2 + \phi(i, j+1)^2 + \phi(i-1, j+1)^2)\right]$$

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where θ is a parameter and Rule 1 is transformed into a simple probabilistic decision of moving toward nearest nodes regardless of the state of that node. These other choices gave basically the same results.

3 Search Algorithm

In this section a simple search algorithm is introduced as a method of finding best-fit solutions. Most search approaches are based on genetic algorithms [8] but here a simpler method is used [7]. To explore the five-dimensional parameter space $(q, \mu, \delta, \sigma_1, \sigma_2)$ in search of possible optimal solutions, we need first to define a fitness measure that somehow takes into account that the maximum number of food items must be brought in at the smallest cost for the colony.

The search algorithm operates on a number of G generations. Each generation consists of N_s runs of the model, starting from a random set of parameter combinations. There is one parameter combination for each of the N_s candidate "solutions," denoted by i. Solution i is described by a five-vector $(q_i, \mu_i, \delta_i, \sigma_1(i), \sigma_2(i))$. During a run of the simulation, which is performed on a 200×200 lattice, the following quantity is estimated over the $T = 1{,}000$ steps of the run:

$$F_i = \sum_{t=1}^{T} \frac{\alpha_{\text{nest}}^t}{N_{\text{ants}}^t} \tag{4}$$

i.e., at each time step t we measure the amount of food entering the nest (α_{nest}^t) divided by the total number of ants in the arena (N_{ants}^t). This fitness measure introduces a reward proportional to the collected resources and a penalty proportional to the number of individuals involved in the search/recollection process.

We start by using $N_s = 16$ candidate solutions that are (uniformly) generated at random from the following intervals: $1 < q_i < 50$, $0 < \mu_i < 50$, $10^{-3} < \delta_i < 1$, $0 < \sigma_1, \sigma_2 < 1{,}000$. We run each simulation and compute the associated fitness F_i $(i = 1, \ldots, N_s)$. Then a selection process is applied following the search method of Marín and Solé [7]:

1. Let $F^* = \frac{\sum_{j=1}^{N_s} F_j}{N_s}$. Solutions such that $F_j < F^*$ are removed from the system (these are called extinct solutions). If there are N_e extinct solutions we should find N_e new solutions to get again a complete population of N_s solutions. This may be done in two different ways:
2. With probability $1 - \tau$, a given extinct solution (say the kth one) is replaced by one of the survivors (say the jth one). All parameters are then modified by a small multiplicative amount ϵ. If β_k is the new value of one of the parameters of the new solution, it is updated as $\beta_k = \beta_j(1 \pm \epsilon)$. If the new value is such that $\beta_k < \beta_{\min}$ or $\beta_k > \beta_{\max}$ then we set the new value to $\beta_k = \beta_{\min}$ or $\beta_k = \beta_{\max}$, respectively. The survivor is chosen at random.
3. With probability τ, a totally new random solution is generated.

The previous rules (here $\tau = 0.2, \epsilon = 0.2$) allow one to explore systematically the high-dimensional parameter space. They have been shown to be very effective for a variety of fitness landscapes [7].

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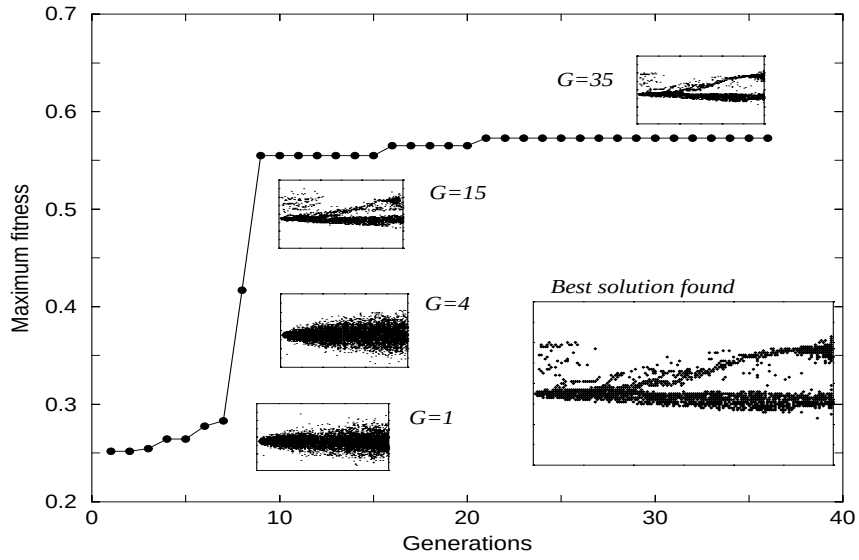


Figure 2. Solutions found in the case of large but rare food sources. This case would correspond to *Eciton hamatum* colonies. Note the random-walk shape found for small G (first generations). The best solution found is consistent with *E. hamatum* raid patterns. See Table 1 for parameter values.

4 Results

Three series of numerical experiments were performed using different combinations of food sources. Let P_f be the probability that a site be occupied by a food source of size F (in arbitrary units). The following cases have been considered: (a) $P_f = 0.01, F = 200$ (e.g., wasp colonies, large but relatively rare); (b) $P_f = 0.5, F = 1$ (e.g., scattered arthropods, common but small) and (c) $P_f = 0.25$ for $F = 1$ and $P_f = 1.25 \times 10^{-3}$ for $F = 200$ (e.g., a combination of scattered arthropods and social insect colonies). All situations are simulated with the same total amount of resources. Here $N_s = 16$ candidate solutions are evolved at each generation. In spite of the small number of solutions used, different simulations gave [for each (F, P_f)] the same average parameter values. For the first case, which would correspond to *Eciton hamatum* colonies, the search algorithm typically starts finding poor-fit solutions with random walk behavior for individual ants (as we can see in Figure 2). In fact the envelope of the raid pattern ($G = 1$–4), as shown in the (x, y)-plane, is close to $y = \sqrt{x}$, as expected for a set of random walks. Later on ($G = 15$) we can see that the algorithm finds a solution displaying some short trails and a few generations later a multiple-trail pattern with a small amount of noise (as indicated by the ants scattered around large trails). This pattern is consistent with those characteristics of army ants feeding on large but rare food sources: Only a few trails are observed.

When another, very different situation is considered we find a rather different optimal search pattern, as is shown in Figure 3. Now the algorithm (after some random-like patterns, see $G = 1$–4) finds branched solutions with many dendrites. Again, this corresponds to the foraging trails found in army ant species like *E. burchelli.* This dendritic pattern is in fact a fractal, and estimations of its fractal dimension give values of the fractal dimension D_f in the range $1.5 < D_f < 1.7$. Finally, for the intermediate case we observe a mixed situation (Figure 4): The system finds an optimal solution that is

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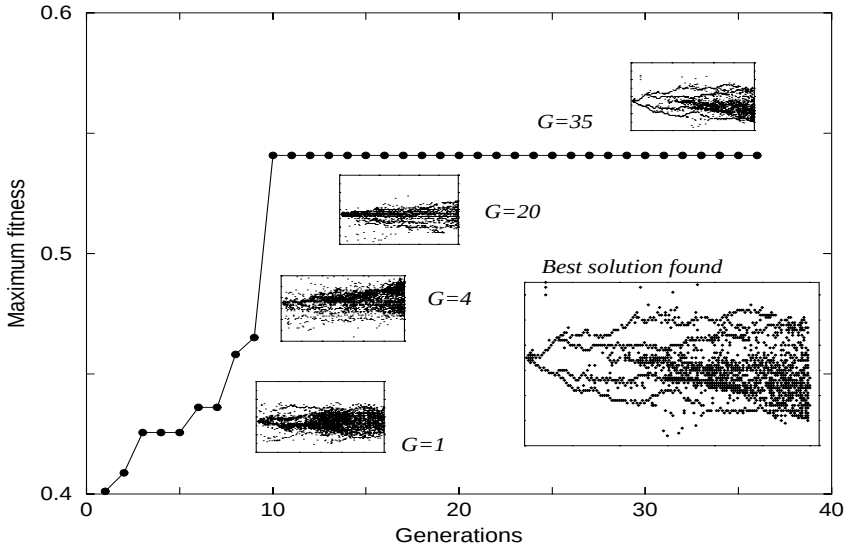


Figure 3. Solutions found in the case of small and frequent food sources, which would correspond to *Eciton burchelli* colonies. Again, the best solution found is consistent with *E. burchelli* raid patterns. See Table 1 for parameter values.

neither a single branch nor a set of well-separated dendrites. Clearly, an intermediate solution is found (although less fit than the previous ones), similar to the pattern observed in *E. rapax*. The parameter combinations obtained for the three different cases are summarized in Table 1. We can see that in all cases the model finds good solutions that minimize pheromone decay and maximize pheromone laid but also the attractiveness of empty sites. In some sense, it seems that a good strategy needs to both guarantee a persistent chemical trail and also to enable some flexibility to facilitate the exploration of new sites. We can also see that the main differences arise from the values of the pheromone saturation parameters: σ_1 and σ_2. In all cases, however, $\sigma_1 < \sigma_2$.

5 Discussion

The results described in this article are important for several reasons: The patterns obtained through a plausible optimization procedure are strikingly similar to those observed in real colonies. That the simulated patterns have been obtained consistently in three different "ecological" conditions provides strong evidence that both the underlying model and the optimization procedure are appropriate.

The results show that different optimal patterns, in different conditions, can be obtained with similar values of the parameters, except for the two pheromone saturation parameters, σ_1 and σ_2. These two parameters may have been the two parameters tuned by evolution to make different species of army ants adapted to their respective ecological niches, represented here by spatial food distributions. This result is an important addition to Deneubourg et al.'s [4] work: These authors showed that it is in principle possible to obtain the observed patterns with a single set of parameter values but they did not *quantify* the patterns in any way; while we were not able to quantify the spatial patterns per se, we did quantify their impact on foraging efficiency and did not rely solely on the eye of the beholder. The result of our more accurate quantification of the patterns is that different sets of parameter values are required to generate optimal

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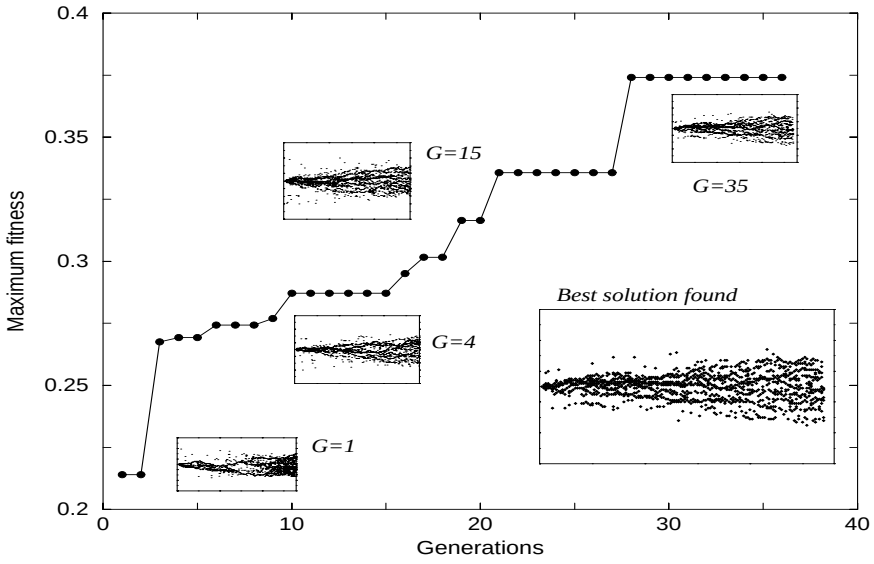


Figure 4. Solutions found for an intermediate configuration of food sources. *Eciton rapax* colonies are the natural analog of this case, with intermediate raid patterns between *E. hamatum* and *E. burchelli*. See Table 1 for parameter values.

Table 1. Results of the search algorithm. For each case, optimal parameters are indicated.

Parameter	σ_1, σ_2	q	δ	μ	Spatial pattern
Large, rare sources	431, 592	46	2.5×10^{-3}	47.5	Single trails
Poor, common sources	51, 390	47	2.1×10^{-3}	47	Fractal
Intermediate	72, 675	50	3.2×10^{-3}	48.5	Few trails

patterns in different conditions, and we have identified which parameter values should be significantly different.

That $\sigma_1 < \sigma_2$ is interesting because it translates into what is observed in army ants: Army ant foragers lay pheromone while advancing with the swarm but to a lesser extent than when returning to the bivouac with prey. Although this inequality may not look like a surprising property since it makes sense to reinforce exploitation trails more than exploration trails, it is reassuring to find it as a natural consequence of maximizing the foraging efficiency of the swarm.

Also, it makes sense to establish stronger trails to larger food sources, which is reflected in the large values of σ_1 and σ_2 obtained for large but rare food sources. For a given evaporation rate, lower rates of pheromone deposition lead to more flexibility, which may be useful when dealing with small, scattered food sources. A prediction of our study is that swarm raiders in *E. hamatum* should lay significantly more pheromone than in the other two species.

Assuming that the model reflects indeed what the ants do, which seems to be confirmed to a certain extent by a remarkable set of experiments [5], this suggests that self-organized raid patterns have been optimized in the course of evolution. Since raid patterns emerge out of relatively simple rules followed by individuals, it means that colony-level selection has shaped the behavior of individuals in such a way that individuals self-organize to implement optimal foraging strategies. Variation at the

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level of individual genotypes has been expressed in colony-level patterns through self-organization.

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