

Mathematical Modelling on Avoidance-to-Acceptance Transition in Leaf Cutting Ant Colonies

J. Amudhavel^{1*}, C. Kodeeswari¹, S. Jarina¹, S. Jaiganesh² and B. Bhuvaneswari³

¹Department of CSE, SMVEC, Pondicherry - 605107, Tamil Nadu, India;
info.amudhavel@gmail.com, kodeeshwari21@gmail.com, jarifathi14@gmail.com

²Department of CSE, R&D Centre, Bharathiar University, Coimbatore - 641046,
Tamil Nadu, India; ggsjaiganesh@gmail.com

³Department of CSE, Pondicherry University, Pondicherry - 605014, Tamil Nadu, India;
info.bhuvnaeswari@gmail.com

Abstract

Background/Objectives: To analyze the behaviors of Forager ants and to utilize some form of memory as a warning system of possible harm to all other members of a colony. **Methods/Statistical Analysis:** Ants acquire experiential memory within a generation. Experience is shared among members of the colony. For instance, knowledge about an unsuitable leaf is shared by means of avoidance, which is subsequently reinforced by autocatalysis. The loss of avoidance thus marks the loss of past knowledge of the unsuitability of a set of leaves. **Findings:** In this research, the highly social behavior of ants, a colony appears to act as a collective entity that is more than the sum of its parts. An individual ant to possess the level of intelligence that enables complex decision-making, the colony made up of such individuals appear to exhibit such complex task. The interactions between individual ants in the colony seem to synchronize with each other and align with group tasks. Ants interact with one another by means of basic signaling protocols, such as trophallaxis among leaf-cutting ants. **Applications/Improvements:** The system has capacity of the ant colony to exhibit transitions from one collective decision and colony memory to the next. The colony of leaf-cutting ants can switch from avoidance to acceptance of leaves which had been deemed unsuitable due to the presence of unwarranted chemical compounds. The transition is not as gradual as one would expect but rather abrupt as evident in the intake rates measured.

Keywords: Ant Colonies, Decision-Making, Leaf-Cutting

1. Introduction

For humans, the concept of learning by experience and subsequent storage of such learning in the memory seem too obvious to deserve any technical attention by common households. For many people, individual learning is indeed a complicated task; how much more is learning in the scale of a society. A society progresses because knowledge accumulated by a certain generation is stored and passed on to later generations through writing and other modes of communication. The body of knowledge is a compendium of human experiences. Ants, however, may have a more primitive form of communication but

certainly do not have a body of knowledge passed on from one generation to the next.

Previous work¹ discusses about the tendency of ants to avoid leaves which are considered unsuitable. The avoidance response can be interpreted as a survival strategy, wherein a worker ant uses its capability to detect unpalatable fungus to discern whether or not a particular leaf is suitable for sharing to the colony. The important finding reported in this study is not so much about the ability of the ants to detect unsuitable leaves, but rather about the apparent capacity of these insects to decide (somewhat intelligently) as a colony when to accept and take in those previously avoided leaves again.

*Author for correspondence

Due to the highly social behavior of ants, a colony appears to act as a collective entity that is more than the sum of its parts. In other words, while we do not consider an individual ant to possess the level of intelligence that enables complex decision-making, the colony made up of such individuals appear to exhibit such complex task. The interactions between individual ants in the colony seem to synchronize with each other and align with group tasks. Ants interact with one another by means of basic signaling protocols, such as trophallaxis among leaf-cutting ants². The emergent property of colonies is certainly interesting because it has far-reaching implications in terms of many relevant aspects of humanity. For instance, the question of why the brain exhibits the properties of consciousness cannot easily be deduced by looking at an individual neuron cell nor an individual dendrite. An ant can sense and respond to its immediate environment and to its local neighborhood. Therefore, an individual ant is able to modify its behavior by focusing on the actions of other ants in the immediate vicinity. In this manner, the ants could focus on which behaviors they need reacting to. This mode of response has been referred as allelomimesis by some authors, and has been put forward as an underlying mechanism for self-organization.

The interesting finding of is the capacity of the ant colony to exhibit transitions from one collective decision and colony memory to the next⁴. The colony of leaf-cutting ants, as observed by Saverschek et al., can switch from avoidance to acceptance of leaves which had been deemed unsuitable due to the presence of unwarranted chemical compounds. The transition is not as gradual as one would expect but rather abrupt as evident in the intake rates measured by the intake rates are initially low because the ants had prior exposure to unsuitable leaves². The rates that ensued are more or less the same on average over the last 12 weeks, after which the intake rate increases fast as more and more ants take in the leaves. The fact that the transition from avoidance to acceptance is not gradual warrants scientific explanation indeed.

A possible mechanism for the abrupt increase of intake rate is autocatalysis. The notion of autocatalysis is that the more individuals in a population are doing a particular action, the likelier it is that new entrants would follow suit. In the context of the ant colony in regards to the avoidance-acceptance transition, the abrupt increase in the intake rate is due to the autocatalytic recruitment of more ants to do a particular action considered previously as harmful and unfavorable. According to the

result concerning the abrupt transition from avoidance to acceptance as indicated by the intake rate may be possibly attributed to demographics³. The motivation behind that speculation is the seeming coincidence between the timing of that transition and the average lifetime of a forager of the *Atta* species. It may also be possibly due to the fact that individuals are influencing one another. This last piece of speculation is also the most salient⁴.

2. Methodology

Ants acquire experiential memory within a generation. Experience is shared among members of the colony. For instance, knowledge about an unsuitable leaf is shared by means of avoidance, which is subsequently reinforced by autocatalysis. However, the knowledge is apparently lost in the next generation, or when a new batch of ants are injected into the colony. Saverschek et al. experiment quantifies learning in terms of the extent of avoidance of unsuitable leaves. The loss of avoidance thus marks the loss of past knowledge of the unsuitability of a set of leaves. In order to further validate some results and observations in that experiment, a mathematical is here formulated. The advantage of the model are its ease of implementation, and the convenience by which numerous replicates can be generated. It is also easier to control unessential and external variables in the mathematical model.

3. Definition of the Model

The main problem that will be addressed by mathematical modeling is finding out the extent that the avoidance-acceptance transition (in terms of intake rates of previously unpalatable leaves) could be explained by autocatalysis. In this paper, autocatalysis is interpreted exactly as the phenomenon in which individuals influence each others' decisions. Moreover, the model must conform to the perceived significance of the timescale of observation (18 weeks) and the role of the lifetime of an individual forager in explaining the intake-rate data.

On the basis of the long-term memory experiments conducted in⁴, the model considers two mutually exclusive actions: avoid and accept. Avoidance by an ant is based on memory of a past encounter with a leaf of unsuitable condition. Acceptance, on the other hand, is interpreted as the opposite of avoidance and is considered to be the default action of a forager without prior memory of the past condition of the leaf.

Let the size N of the colony be very large (i.e., $N \gg 1$) so that the population concentration would serve as an appropriate quantity for describing the colony in mathematical terms. Hence, let x and y be the concentration of ants which accept and avoid, respectively. Further assuming that the observation time is much longer than the average time of encounter between two ants, then the rates of change of x and y could be expressed as a system of two first-order ordinary differential Equations:

$$\frac{dx}{dy} = a - bx + cxy \quad (1)$$

$$\frac{dy}{dt} = -cy - by \quad (2)$$

The rate a in Equation (1) represents the injection rate of new ants who have no prior memory of the condition of the leaf. In other words, this is the rate of replenishment of naive ants into the colony. The rate b denotes the average mortality rate of a forager, which Saverschek et al. pointed out in their paper to be a large unknown with scanty research on measuring it. Lastly, c represents the average rate that acceptance ants are able to influence an initially avoidance ant to switch. In other words, it is assumed in the model that the switching from avoidance to acceptance requires at least an encounter between these two types of ants, the probability of which is represented by the product of the concentrations x and y . The model does not consider any spatial geometry in order to keep it as simple enough as possible. Hence, the product xy is sufficient enough to describe the mean encounter rate between different types.

Equations (1) and (2) form a two-dimensional system of first-order differential equations. Equation (1), in particular, is inhomogeneous due to the presence of a source term $a > 0$. On the other hand, Equation (2) is a homogeneous equation and would require the coupling with equation (1) in order to keep from evolving towards the null solution $x = 0, y = 0$.

The rates a, b , and c are the free parameters of the model. Due to these parameters, the model is not easy to relate with the real problem. Hence, a reduction of parameters is required. Through reduction, only the essential parameters are retained in the system therefore decreasing the degrees of freedom. The following similarity transformation is performed to reduce the number of parameters in the system made of equation (1) and (2).

4. Similarity Transformation and the Essential Parameter of the Model

Because of the unknown average mortality rate, it is best to perform a similarity transformation of the model in order to reduce any unessential parameters. The similarity transformation is given as follows:

$$x = \varepsilon^q \bar{x}, y = \varepsilon^r \bar{y}; t = \varepsilon^\tau \bar{t}$$

$$a = \varepsilon^\alpha \bar{a}; b = \varepsilon^\beta \bar{b}; c = \varepsilon^\gamma \bar{c}$$

which by application to the given

$$\varepsilon^{q-r} \frac{d\bar{x}}{d\bar{t}} = \varepsilon^\alpha \bar{a} - \varepsilon^{\beta+q} \bar{b} \bar{x} + \varepsilon^{\gamma+q+r} \bar{c} \bar{x} \bar{y}$$

$$\varepsilon^{r-r} \frac{d\bar{y}}{d\bar{t}} = -\varepsilon^{r+q+r} \bar{c} \bar{x} \bar{y} - \varepsilon^{\beta+r} \bar{b} \bar{y}$$

The invariance of the rescaled equations to the similarity transformation implies the following conditions relating the different exponents to the scaling parameter.

$$q - r = \alpha = \beta + q = \gamma + q + r$$

$$r - r = \beta + r = \gamma + q + r$$

Based on the above equations, it is possible to deduce the following:

$$q = \alpha - \beta = r$$

$$\gamma = 2\beta - \alpha$$

which implies further that

$$\xi = \frac{b}{a} x; \psi = \frac{b}{a} y; C = \frac{a}{b^2} c \quad (3)$$

so that the dimensionless system could now be written as follows:

$$\frac{1}{b} \frac{d\xi}{dt} = 1 - \xi + C\xi\psi \quad (4)$$

$$\frac{1}{b} \frac{d\psi}{dt} = -C\xi\psi - \psi \quad (5)$$

wherein the essential parameter is C , and the time scale under consideration, $b dt$, is proportional to the mortality rate of ants. The time scale of the model can therefore be set such that $bdt = 1$.

5. Results and Discussion

The rescaled system consisting of Equation (4) and (5) is analyzed. The essential parameter C is used to classify the solutions and for comparison with the real problem as described earlier⁴.

5.1. Analysis of the Model

In order to analyse the model⁴, the values of a and b are considered to be numerically equal so that $C = c/b$. Thus, the essential parameter C indicates how fast the switching interactions are (as represented by the rate c) with respect to the mortality rate of the ants.

By simultaneously solving the dimensionless system such that the two derivatives are set to zero, the deterministic fixed points of the system is determined to be $x^* = 1$ and $y^* = 0$, which represents the state wherein the entire colony consist of acceptance ants. In order to find out whether or not the said equilibrium solution is stable, the Jacobian matrix of the system is evaluated at the fixed point. Although not any more shown here, it can be verified that evaluating the Jacobian would imply that the fixed point is a stable one. Thus, after a long time, the solution to the system is expected to converge to a state of long-term acceptance, as anticipated by Saverschek et al⁴.

5.2. Existence and Uniqueness of Solution

The dimensionless³ system can be shown to have a unique (maximal) solution in the domain corresponding to the set of real numbers in 2-dimension. Consider the initial condition $t = 0, x = 0, y = 1$, which mimics the conditions used by Saverschek et al. in their long-term memory experiment. Obviously, the triple $(t, x, y) = (0, 0, 1)$ is an element of the domain of the system.

Meanwhile, the right-hand side of the two equations in the dimensionless system are continuous by virtue of being polynomials or products of polynomials in both time and space. The partial derivatives of the right-hand side of the two equations with respect to the dependent variables x and y could also be shown to be continuous over the domain of the system.

Therefore, the dimensionless system has a unique solution over its domain. In other words, for every unique initial condition, there is one and only one solution curve that will connect one point to another in the domain. Because of the existence of such unique solutions, it is now guaranteed that numerical approximations to the

solution of the model, with certain conditions regarding accuracy and precision, are guaranteed to converge to the analytic solutions.

No attempt has been made here to determine a closed-form analytic solution, although it can be easily obtained. Instead, in order to directly visualize the solutions, numerical method has been used for solving the Equations (4) and (5) simultaneously for a given set of parameters.

6. Numerical Solution

The parameter values used in the numerical solution are $a = b = 0.000008$ and $c = 0.8$, so that the essential parameter $C = 100,000$. Owing to the large value of the essential parameter, the system would be practically stiff. The solution is numerically implemented using MatLab software using the stiff differential-equation solver ode23s. The result of the simulation is illustrated in Figure 1.

Indeed, the numerical solution² reveals that the level of acceptance abruptly increases after a certain time has been reached since the addition of external naïve ants, which do not have any memory of the past condition of the leaf. The abrupt transition at about $t = 15$ weeks is determined by the parameter settings. The transition is shifted by changing the parameters.

Acceptance eventually takes over in the colony as time progresses because there is an inherent tendency of the ants to forage whatever food is available in their surrounding. Due to that bias, avoidance is expected to

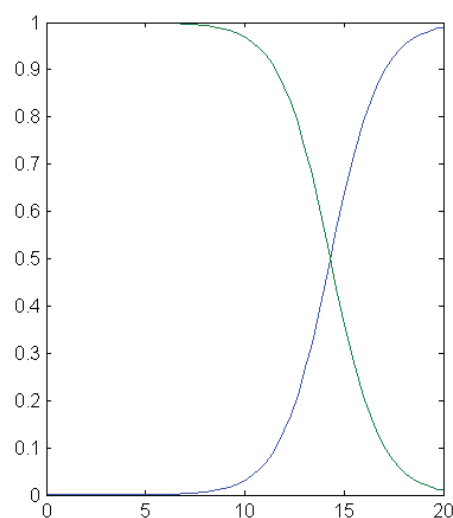


Figure 1. Percentage of ants displaying avoidance and acceptance behaviors.

transform into acceptance. The autocatalytic interaction⁵ represented by the product xy is an important element in the model that determines the time in which the level of acceptance abruptly increases.

What the outcome of the simulation reveals is that knowledge acquired by learning through encounters with unsuitable leaves is retained within a generation and within a colony. However, when new ants are introduced into the population, which simulates immigration, the knowledge is not transmitted. It would be expected that knowledge will be lost from one generation to the next. Avoidance behavior is interpreted as evidence of learning. Starting at the level wherein all ants display avoidance behavior, that level suddenly drops after a certain amount of time that new ants, which had no prior encounter with the unsuitable leaves, are injected into the population.

Figure 1 represents the population of ants (%) displaying avoidance and acceptance behaviors. The solution is obtained by solving Equations (4) and (5) in Matlab. The horizontal axis denotes the time (in weeks), whereas the vertical axis denotes the concentration of a particular type of ant. The blue (increasing) graph corresponds to the concentration of acceptance ants, x . The green (decreasing) graph corresponds to the concentration of avoidance ants, y .

The model is not without limitations. The essential assumption in the model is that the ants are well mixed in the colony, and that the colony is very large. In the future, it is recommended that a suitable description for finite-size effects be incorporated into the proposed model for the purpose of adding more realism into it. However, it is expected that the general results would still hold even in that modified system.

7. Summary and Conclusion

Humans transmit knowledge acquired from one place to another, and from one generation to the next by means of memory storage and communication. Ants, on the other hand, show no evidence of that retention of knowledge across time and space. Ant populations have been used as experimental systems to do research on learning behaviors. An article by Saverschek et al. reported about an experiment to confirm whether or not knowledge is retained socially, and if not, for how long does it last. The experiment showed that memory lasts for about 15 weeks before it is totally lost in a rather drastic way.

The abrupt transition is possibly because of autocatalysis. A mathematical model has been formulated to

explore that hypothesis. The model considered two variables that represent the fraction in the population of ants that hold acquired knowledge (avoidance behavior)⁶, and those that do not (acceptance behavior)¹. Initially, all ants in the population display avoidance behavior. Over time, new ants, which do not hold the knowledge, are injected into the population. The mathematical model does show that the level of avoidance is maintained close to the initial level of 100% for a length of time. But after about 15 weeks, that percentage quickly drops to almost 0% in a matter of days. The abrupt transition, as observed through simulations of the model, is exactly similar to the one observed in actual experiments.

Despite the complexity of ant behavior, it is possible to extract only essential details to obtain a minimal mathematical model that is able to explain emergent phenomena in ant populations. Mathematical models serve as time- and cost-efficient platforms for testing hypotheses about complex behavior. Quantitative socio-dynamics is a budding field reinforced by the existence of unprecedented computational power, which should be used to tackle more difficult mathematical problem-solving tasks than ever before.

8. References

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