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Mathematical Modelling on Nutrient Transmission in a Colony of Leaf-Cutting Ants

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Abstract

Background/Objectives: To analyze the Nutrient diffusion through an ant colony is a complex process of transmitting information from one node to another. **Methods/Statistical Analysis:** Ants have a special mode of transmission known as trophallaxis, which involves the transfer of liquid-based food from one ant's mouth to another. The worker ants may be categorized into two types: forager and non-forager, both of which are involved in the food transfer. **Findings:** In this research, by considering trophallaxis, the diffusion of the food signal through the ant colony is modelled as a two-type branching process. Analytic results based on asymptotic estimates of the branching process are here shown to be consistent with empirical results gathered from mini-colony experiments. The division of labor in worker ants is an important feature that exhibits the sociality of the colony. Indeed, resource allocation becomes more efficient if each worker ant is able to focus on one particular task only throughout its lifetime. **Applications/Improvements:** The division of labor, forager ants tends to be the more “aggressive” type in terms of seeking ants from which food can be received and subsequently exchanged. Meanwhile, the non-forager ants are more specialized in nest-maintenance activities and because of their relatively smaller size are more likely to obtain nourishment by another means. The trophallactic transmission process is investigated by Moreira et al. by conducting an experiment on a mini-colony of ants consisting of a mixture of the two classes[3].

Keywords: Leaf-Cutting, Nutrient, Trophallaxis

1. Introduction

The transmission of information is an important issue in communication networks. Understanding the dynamics of information diffusion may present to us facets of communication we have never known through our own human experience. Animals could possibly teach us a thing or two about communication, such as how to make it more efficient and less energy consuming. Evidence of social behavior in creatures such as honeybees and ants testify the fact that humans do not own the exclusive ability of meaningful communication. Ants, in particular, are known to have poor eyesight. Yet, they are capable of finding food and eventually pass it on to the queen who is deep inside the colony.

In a paper by[1] in the Journal of Insect Physiology, 1a description of nutrient diffusion in an ant colony is described in terms of a classification of worker ants into two types, namely, foragers and non-foragers. The foragers are distinguished from non-foragers by virtue of capsule size, hence the capacity to store liquid-based nutrients. The differentiation between foraging and non-foraging ants is thus a matter of physiology.

Study reveals that despite the presence of two distinct types of leaf-cutting ants in a colony, there is an efficient transmission of nutrient within the colony. The mode of

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transmission is referred as *trophallaxis*, which involves the transfer of liquid-based food from one ant to another. The division of labor in worker ants is an important feature that exhibits the sociality of the colony[2]. Indeed, resource allocation becomes more efficient if each worker ant is able to focus on one particular task only throughout its lifetime. The finding by is that, because of division of labor, forager ants tend to be the more "aggressive" type in terms of seeking ants from which food can be received and subsequently exchanged. Meanwhile, the non-forager ants are more specialized in nest-maintenance activities and because of their relatively smaller size are more likely to obtain nourishment by another means. The trophallactic transmission process is investigated by conducting an experiment on a mini-colony of ants consisting of a mixture of the two classes.

Here, the study is explored quantitatively using the mathematical modeling approach[3]. The observations made on the behavior of the worker ants in regards to foraging are accounted for in the most mathematical way possible. The motivation for implementing such approach is that studying ant behavior mathematically is a more efficient method for exploring[2] various scenarios. Such exploration is difficult (if not impossible) to conduct with actual ant colonies. Mathematical modeling may also provide useful insights for developing robotic swarm systems that communicate in a similar manner as ant colonies.

2. Methodology

In the mini-colony experiment, an initial donor (an ant carrying liquid-based food) is placed into the pre-existing colony inside a petri dish. The clever approach which the authors did in their experiment is to mix the liquid food (made of honey) with a non-toxic dye that will serve as a marker. The purpose of the marker is to track the exchange/transmission of the liquid food from one ant to another. Hence, determining the path of transmission can be visually shown; for instance, it can be known which type of ant transfers food to another type. The authors have been able to present statistics with regard to the transmission dynamics.

The data obtained by study reveal that foraging ants are those for which the dye has been frequently detected. On the other hand, a relatively smaller proportion of non-foragers have been detected with the dye. In more quantitative terms, about 32% of the foraging ants have been detected to carry the dye tracer at the end of 10 hours; whereas, an average of only about 5% of non-foraging ants have been detected as carriers of the tracer. Comparing those percentages would imply that foragers are those ants which were mostly active in the trophallactic transmission process in comparison with non-foragers. That is, of course, not a surprising result if one considers the fact that foragers are specialized to transmit nutrients from source to the nest[4].

The motivation behind the 10-hour observation time is a previous study which found that the average time between ingestion of liquid food to excretion through the rectum is about 10 hours. Hence, the experiment conducted by Moreira et al. considers that trophallaxis should occur within 10 hours if the purpose for that process is to transmit food from one ant to another until that food reaches the nest, where the queen ant, the most important member of the colony, resides. What is more revealing about study is the possibility that the mode of nutrient transmission of ant colonies may be exploited as an effective means of dispersing insecticide to eradicate ants. In some settings, leaf-cutting ants are considered as agricultural pests. Hence, a less costly but effective insecticide distribution is necessary and most sought after.

3. Preliminary Calculations based on Experimental Data from Moreira et al.

In order to appreciate the significance of the findings from Moreira et al.[3], some calculations are done on the basis of the data obtained from that study. They said report; about 240 ants were placed in the mini-colony. Non-foragers outnumber foragers in that mini-colony by a ratio of 5:3. Ants of different types which carry liquid-based food (with the dye tracer) are then placed into the mini-colony. From that point in time until 10 hours after, the ant colony was left on its own as the ants interact with one another. The ants had the time to exchange food via trophallaxis before the food gets processed and subsequently excreted by any single ant. At 10 hours, the colony was frozen hence killing the ants. The dead ants thus preserve any trace of the dye inside their digestive tracts. The ant bodies were then dissected to reveal the presence of the tracer.

According to the findings, about 32% of the foraging ants were detected to have the tracer; whereas only 5% of the non-foraging ants had the tracer. As a result, about 58 of the total ant population had been detected with the dye at the end of 10 hours. About 29 of those 58 ants, or 50%, were foragers. Considering that there were more non-foragers in the mini-colony, the result of 50% foragers with the dye after 10-hours supports the hypothesis that nutrient transmission from one ant to another was mostly participated by foraging ants.

To sum up the above calculations, let us consider the two most essential quantities. One is the observation time which corresponds to the lifetime of the nutrient (hence, the dye) within the digestive system of the ant. Let,

$$\delta = 1 \textit{ per } 10 \textit{ hours}$$

be the average rate for which a quantity of the ingested liquid nutrient is dissipated out of the population via excretion[3]. Another important quantity is the ratio of foraging ants which had participated in the trophallactic transmission as revealed by the presence of the dye tracer after 10 hours. Let this ratio be defined as,

$$\rho = \frac{1}{2}$$

The goal of the present study is to use a mathematical model to describe the nutrient transmission process in an ant colony by means of trophallaxis. The motivation for devising a mathematical model is so that an insight can be gained in regards to the necessary conditions for such transmission to be efficient. By uncovering certain aspects of the transmission, we might realize how important trophallactic transmission is later on for the dispersal of insecticide baits. Analysis of the mathematical model might provide estimates concerning the damage that insecticides would do if transmitted by way of trophallaxis in an ant colony.

4. Formulation of the Mathematical Model

The trophallactic transmission in a colony can be interpreted mathematically as a two-type branching process. The motivation for such interpretation is an earlier work on termites where the phenomenon referred as "trophallactic cascade effect" had been proposed as an explanation of the transmission dynamics. The mathematical problem is determining the proportion of ants involved in the trophallactic transmission of food within a given amount of time (e.g., 10 hours).

In order to formulate the model, let us first lay out some important assumptions which would aid in simplifying the mathematics sufficiently as to be solvable. Let F denote foraging ants, and G denote the non-foraging ones. Furthermore, let f and g denote the number of foragers and non-foragers, respectively, which are carrying the nutrient at a given time t. The nutrient diffusion through the colony as a two-type branching process may be expressed as a system of reaction equations:

$$F \rightarrow F + F withrate\ \lambda$$
$$F \rightarrow F + G withrate\ 1 - 2\lambda$$
$$F \rightarrow G + G withrate\ \lambda$$
$$G \rightarrow \phi\ withrate\ \delta$$

Equation (2) denotes the sharing of food by a foraging donor with a foraging recipient at a certain rate. Equation (3) represents the sharing of food from a foraging donor to a non-foraging recipient. Equation (4), on the other hand, represents the full transfer from a forager to two non-foragers (like depositing all collected food into the nest). Finally, Equation (5) represents the delivery of food from a non-forager to the end user in the colony (usually the queen).

The use of a formalism borrowed from writing chemical equations has been a common way of describing an event-driven model. The formalism lays out clearly what processes are involved, and which components (or component types) are being changed in each process. In a sense, the events described are fundamental to the model itself. Methods based on differential equations usually skip the step of describing, in an algorithmic fashion, the relevant events of processes. In this study it is not skipped because the mathematical problem is treated as being stochastic, rather than deterministic. The stochastic nature of the problem emphasizes the contribution of discrete events, processes, and components toward the mathematical solution. Most importantly, the formulation of the model in terms of a formalism applied onto Equations (2) to (5) leads to a straightforward representation of the stochastic problem using what is known as the master equation. From this equation, many qualities of the behavior of the solution can be explored and analyzed.

5. Results and Discussion

Let $P(f,g;t)$ denote the probability that at a given time t there are f foragers and g non-foragers which are carrying the liquid food. The said probability satisfies the following master equation:

$$\frac{dp(f,g;t)}{dt} = (f-1)\lambda P(f-1,g;t) + (1-2\lambda) fp(f,g-1;t) + (f+1)\lambda p \\ (f+1,g-2;t) + (g+1)\partial P(f,g+1;t) - (\partial g + f)P(f,g;t)$$

Equation (6) is actually an exact differential equation but not always solvable in general. In order to make it solvable, further simplifications of the model have to be made.

The model could further be simplified on the basis of the findings of Moreira et al. that non-foragers are not particularly essential during the trophallactic transmission, at least in the context of their experiment[4]. In other words , the two-type branching process could be reduced to a one-type critical branching process that only considers the foragers. The reduced process is thus:

$F \to F + F$ *withrate* λ
$F \to \phi$ *withrate* λ

The initial condition, in accordance with the mini-colony experiments should involve the introduction of ants that carry liquid food. Let us consider only one of such initial donor. Hence, the initial condition for the initial value problem of the master equation may be specified as follows,

$$P(f, g; 0) = \delta_{f,1}\, \delta_{n,0}$$

where δ represent the Kronecker delta symbol which has the value of zero in general except for the case wherein the two indices are equal, and should not be confused with the rate "delta". The fundamental interest is of course the solution to the probability distribution $P(t)$. Let $s = f + g$ so that the reduced probability distribution can be written as the sum of the probabilities accounting for all possible combinations of f and g.

Based on the simplified model, the initial condition may also be only written as

$$P(f; 0) = \delta_{f,1}$$

representing the condition that there is only one donor in the beginning. The solution to the master equation can be stated as a piecewise function depending on the value of f:

$$p(f;t) = \begin{cases} \dfrac{1}{(1+\lambda t)^2}\left(\dfrac{\lambda t}{1+\lambda t}\right)^{m-1}, form \geq 1 \\ \dfrac{\lambda t}{(1+\lambda t')} \qquad form = 0 \end{cases}$$

Theorem. The expected number f of foragers holding the liquid food at any given time within 10 hours is equal to 1.

Proof. Based on Equation (7) the expected number is defined as follows.

$$\langle f \rangle = \sum_{f\geq 0} fp(f;t) = 0.\frac{\lambda t}{1+\lambda t} + \frac{\lambda t}{(1+\lambda t)^2}\sum_{m>1} m\left(\frac{\lambda t}{1+\lambda t}\right)^{m-1}$$

The second term of the above equation is simply a geometric series, which by assuming that f is unbounded, would further simplify the equations. For convenience, let x represent the quantity inside the parenthesis. Hence, the calculation for the moment proceeds as:

$$\langle f \rangle = \frac{1}{(1+\lambda t)^2}\sum_{m=1}^{\infty} m x^{m-1}$$
$$= \frac{1}{(1+\lambda t)^2}\frac{\partial}{\partial x}\left(\sum_{m=1}^{\infty} x^m - 1\right)$$
$$= \frac{1}{(1+\lambda t)^2}\frac{\partial}{\partial x}\left(\frac{x}{1-x}\right)$$
$$= \frac{1}{(1+\lambda t)^2}(1+\lambda t)^2$$
$$\langle f \rangle = 1$$

The above result is of course consistent with the definition of a critical branching process. A critical branching process is the borderline between super-critical and sub-critical processes. Furthermore, the expected number of non-foragers carrying the food at any moment can be calculated in a similar manner[5]. This quantity should satisfy the following initial-value problem,

$$\frac{d\langle g \rangle}{dt} = \langle f \rangle - \partial\langle g \rangle, \qquad \langle g \rangle(0) =$$
$$\langle g \rangle = \frac{1-e^{-\partial t}}{\partial}$$

Proof. Let <*f*> = 1 so that Equation (8) would now simply be in terms of <*g*> and which could be solved using separation of variables, neglecting the constant solution <*g*> = 1/δ, as outlined in the following steps:

$$\frac{d\langle g\rangle}{dt} = 1 - \partial\langle g\rangle$$

$$\frac{d\langle g\rangle}{1-\partial\langle g\rangle} = dt$$

$$-\frac{1}{\partial} In(1-\partial\langle g\rangle) = t + c$$

$$1-\partial\langle g\rangle = Be^{-\partial t} \Rightarrow B = 1$$

$$\langle g\rangle = \frac{1-e^{-\partial t}}{\partial}$$

Hence, the expected number of ants which hold the resource at any given moment is

$$\langle h\rangle = 1 + \frac{1-e^{-\partial t}}{\partial}$$

Asymptotically, the value of the expected fraction of foragers which are involved in the trophallactic transmission of the nutrient is as follows,

$$\langle \rho_\infty\rangle = \frac{\langle f\rangle}{\langle h\rangle} = \frac{\partial}{1+\partial}$$

Equation (11) represents a result that can (and should) only be associated with measurements taken after a long time since the system had been left in place without intervention. The asymptotic result in in terms of δ is very close to zero when δ → 0. On the other hand, if δ >> 1, the right hand-side of equation (10) would be close to 1.

The outcome of the analysis is best validated through empirical data gathered from a system that is as similar as possible to the one represented by the mathematical model. The assessments made through the validation are discussed in the following section.

6. Validation of Results with Data

Based on the Equation (9) and (10), it is now possible to validate the theoretical description of the trophallactic transmission using the data obtained by using the following values:

δ = 1

which upon evaluating the right-hand side of the equation, would yield

$$\langle \rho\rangle = \frac{1}{2}$$

The calculated values are indeed considerably close to those obtained from the data of Moreira et al. as mentioned in *Preliminary calculations*[5]. The observation period of 10 hours in the mini-colony experiments had been sufficiently long enough to achieve the asymptotic result predicted through the theoretical model. Hence, equation (11) should serve as a sufficient description of the system. It also justifies the approximations made to simplify the model.

Thus, based on the positive result of the validation, it can be said that the mathematical interpretation of the trophallactic transmission of nutrient in the colony[6] as a two-type branching process is quite accurate. The model has been solved by virtue of simplifying assumptions, which may not be entirely consistent with the real problem. For example, the branching process assumes no spatial distribution of the ants in the colony and that the number of such ants is very large. Furthermore, it is assumed that the colony is well-mixed such that any single ant would meet every other ant with constant probability per unit time.

The entire system may be interpreted as a telecommunication or information network wherein the two types of foraging ants represent two types of network participants or nodes. One type includes communicators who have the tendency to pass on or relay to their intermediate connections a piece of message they receive. The other type includes communicators whose instinct is to ignore the message and be concerned not at all. The diffusion of the message through this network does seem to be a branching process[7]. Hence, investigating the transmission of food through a worker-ant population has provided insight into human communication.

7. Summary and Conclusion

The diffusion of liquid-based food through a worker ant network has been explored with the guidance of the empirical study conducted on mini-colony experiments. Trophallaxis has been considered as the mode of transmission, and two categories of worker ants have been accounted for. A mathematical model specified as a two-type branching process has been formulated through the interpretation of the real problem under study.

The analysis of the branching process has revealed several insights that contribute towards understanding the diffusion of information through a network. The two classes of worker ants are different in terms of probability of transmission. Foragers, on the one hand, have the instinct to pass on food to the next worker ant nearby. Non-foragers, on the one hand, do not typically exhibit such behavior. Hence, the transmission of food is not 100% as some of it "leaks out" of the population by virtue of not getting passed on. Indeed, this property of the ant system considered in this paper may be considered a toy model, from which takes off many new insights toward understanding the diffusion of information.

Ultimately, the results on the analysis of the model are validated in terms of the empirical data. The motivation is really to establish the possibility that the model is sufficiently correct as a description of the real problem. Of course, such description is bound to be incomplete and simplified because several unaccountable factors are neglected in the formulation. In this study, such validation has been achieved.

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