



Directional ambiguity in trail-laying algorithms

Tomoko Sakiyama^{a,*}, Yukio-Pegio Gunji^b

^a Department of Intelligent Mechanical Systems, Graduate School of Natural Science and Technology, Okayama University, Okayama, Japan

^b Department of Intermedia Art and Science, School of Fundamental Science and Engineering, Waseda University, Tokyo, Japan



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ABSTRACT

We developed multi-agent models inspired by ant foraging. Previous research shows that ants obey Weber's law and change their moving angles based on pheromone conditions. We constructed trail-laying models in which agents estimate the global pheromone gradients based on local pheromone gradients, which resulting in emergent Weber's law. Agents were also admitted to use directional cues based on motions of other local agents to produce realistic curved paths. We also showed that re-estimation of pheromone gradients based on directional cues yields a balance between exploitation and exploration.

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1. Introduction

Ants use visual landmarks, panoramic cues, path integration, magnetic cues, odors and vibrational information in addition to chemical pheromones to return to their nest or relocate to previously identified food areas (Goss et al., 1989; Wehner et al., 1996; Robinson et al., 2005; Buehlmann et al., 2012; Zeil, 2012; Czaczkes et al., 2014). Some ant species use exploration or trail pheromones as their navigation systems, and nonlinear models have attempted to illustrate ant trail-laying patterns (Deneubourg et al., 1989a, 1989b; Goss et al., 1989; Dussutour et al., 2004, 2006). However, several recent studies have reported that ants appear to linearly react to pheromones at micro-levels (Weber's law) (Perna et al., 2012; von Thienen et al., 2014). Specifically, ants appear to obey Weber's law and move in a certain direction based on the surrounding pheromone concentrations. When ants obey that law, regarding certain pheromone gradients, the moving angle is changed significantly when the total amount of surrounding pheromones is small. In contrast, when the total amount of surrounding pheromones is large, the moving angle is weakly changed. The probability of moving in a certain direction is thus determined by the pheromone concentrations (Perna et al., 2012; von Thienen et al., 2014). This continuous directional change can result in the emergence of nonlinear patterns. Weber's law, as described in related previous research, indicates that ants are sen-

sitive to small pheromone gradients. While obeying Weber's law, ants might estimate the global pheromone gradients by changing the moving angle and pheromone detection areas. There is no model simulating such decision processes of agents. Weber's law is itself a phenomenological result.

To this end, we allowed our simulation agents to detect limited surrounding areas when estimating pheromone amounts by allowing them to weakly use Weber's law. To produce nonlinear patterns, we forced the agents to change the detection areas used for pheromone estimations depending on the environmental conditions.

Moreover, we admitted agents the stopping behavior because ants in an unexplored area are slower than those in a chemical reinforced area and allowed them to go forward constraint. The "going forward constraint" is to model straight trails like the ones done by army ants (Deneubourg et al., 1989a). However, actual trail-laying patterns of foraging ants occasionally illustrate curvatures (Perna et al., 2012). To this end, we also allowed the simulation agents to weakly detect the motions of other local agents with the aim of obtaining curvy, realistic paths, meaning the emergence of paths, which are not straight and do not exhibit extreme curvatures. We assumed that the agents could use alignment matching when a primary cue, i.e., a chemical cue, offered them poor information. This assumption is sensible because such alignment matching has been observed in fish shoals and bird flocks, although no empirical study has demonstrated this behavior in ants (Couzin and Kranse, 2003). We aimed to show that this assumption, even coupled with the rule that agents are forced to move forward, can lead to the emergence of realistic patterns.

* Corresponding author.

E-mail address: tmk.sakiyama@gmail.com (T. Sakiyama).

It might always be difficult for an agent to judge whether to just obey the majority of other local agents through alignment matching or to only consider a minority of other local agents because agents cannot obtain a perfect global spatial perception of profitable locations using only local information. This problem is similar to the problem of global gradients, which local pheromone gradients have. High pheromone gradients do not always offer clear directions to profitable locations. Therefore, it is unclear how an agent estimates the global gradients of local pheromone gradients. To this end, the agents in our model regard pheromone gradients as secure information when a majority of the other local agents are heading in the same direction as the pheromone gradients. However, if at least one agent is going in the opposite direction, the agents ignore the pheromone gradient and regard it as a local biased cue. As a secondary and momentary cue, global gradients in local directional information must be weaker than those of local pheromone gradients. To this end, the global reliability of local pheromone gradients can be either facilitated or inhibited when the majority of other agents are moving in the same direction as the pheromone gradients. This is dependent on the existence of a directional minority of other agents in our model. Thus, the agents in our model flexibly interpret local pheromone gradients based on directional information from other local agents. Based on to this interpretation, the agents in our model can obtain a balance between exploitation and exploration. Many agents can follow a rigid trail while others move away from the main trail path. This type of modulation at individual levels must be important for ants because the flexible nature of the decision-making process of each agent would help achieve a balance between exploitation and exploration at the colony level (Detrain and Deneubourg, 2006).

2. Materials and methods

The Agent-Based Simulation Model

We developed a spatially explicit synchronous agent-based model of ants foraging. Our models were coded by the C programming language. The model description follows the ODD protocol (Grimm et al., 2006, 2010).

2.1. Purpose

The purpose of the model was to establish realistic trail-laying patterns. We added directional information as a cue to permit the emergence of curved paths. We also allowed changes in the moving angles in a certain direction based on the local pheromone gradients when ants updated their positions using pheromone concentrations. We named the proposed model the DP (Direction-Pheromone) model. To evaluate curvature, we developed a P model in which the agents could not use directional information. In addition, to achieve a balance between exploitation and exploration, we developed an alternative model named the improved DP model in which the agents sometimes modulated the changes of their moving angles in a certain direction.

2.2. Entities, state variables and scales

We developed three different models (the DP model, the improved DP model and the P model), and these models include two types of entities: individuals and patches. The individuals have the following state variables: *Navigational state*. The *Navigational state* can have two values: *Navigational state* = {pheromone, direction}.

A patch has the following state variable: *Pheromone*. This value represents the pheromone amount on each patch.

The time and spatial scales differ between the two types of analyses. Thus, we describe their process for each analysis (open field analysis/binary route choice analysis) separately.

2.2.1. Open field analysis

The models consist of a grid of 800 by 800 patches (the environment). The models are temporally explicit and run 1000 time steps. A list of parameters for the agents, patches and global variables is shown in Table S1.

2.2.2. Binary route choice analysis

The agents are forced to move in Y-shaped areas, and the models consist of a grid of square patches (the environment) with a width of 1.00. Therefore, the width of each branch is also set to 1.00. The models are temporally explicit and run 500 time steps. A list of parameters for the agents, patches and global variables is shown in Table S1. Please also see Fig. S1.

2.3. Process overview and scheduling

We describe the process overview and scheduling for each analysis (open field analysis/binary route choice analysis) separately because the scheduling and the sub-models present slight differences between the two types of analyses.

2.3.1. Open field analysis

This scheduling was used for analyses using all three different models (DP, improved DP, and the P model). At each time step, the agents were first allowed to move in the default direction and scanned the pheromone amounts on the three patches in front of them along the default direction (see sub-model “1st estimation”). Note that the actual position was not updated in this sub-model of any of the three models. Thus, each agent could estimate the local pheromone gradients in the default selected patches and directional information. Based on local circumstances, the agents sometimes changed the sets of selected patches after the “1st estimation”. In addition, they sometimes used directional information instead of pheromone information after the “1st estimation” (see sub-model titled “2nd estimation”, which determines the new position of the agents). After “2nd estimation”, the agents update their positions and deposit one unit of pheromone on the new positions (see sub-model titled “position-updating”). Note that additional sub-models were added to “2nd estimation” only for the improved DP model. We named the sub-model “2nd-add estimation”.

2.3.2. Binary route choice analysis

This scheduling was used for the DP and improved DP models. The agents followed only the “1st estimation” and “position-updating” sub-models until they reached a branch point. When arriving at a branch point, the agents were subjected to the “1st estimation”, “2nd estimation” and “position-updating” sub-models. After passing a branch point, the agents again followed only the “1st estimation” and “position-updating” sub-models. Note that additional rules were added to the “2nd estimation” sub-model of the improved DP model to obtain the “2nd-add estimation” sub-model.

2.4. Design concepts

The trail patterns in the case of open field analysis and the proportions of agents at the branches in the case of binary-route choice analysis are the emergent properties of the model. The concepts of adaptation, objectives and prediction are not important in this model, and there is no learning in the model. Sensing is important: agents leaving the nest are able to detect the pheromones left on patches and orient themselves according to the pheromone

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