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Modeling shortest path selection of the ant *Linepithema humile* using psychophysical theory and realistic parameter values

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HIGHLIGHTS

- The Deneubourg model explaining how ants are able to find the shortest of two paths between nest and food source has been tested based on parameters deduced from experiments.
- The Deneubourg model could be confirmed.
- However, the model uses a mathematical choice function describing the decision of ants depending on pheromone concentrations. This choice function has to be exchanged by a psychometric function for the model to satisfactorily explain the shortest path experiments.
- The finding of Aron et al. (1989) that ants modulate their pheromone deposition depending on their direction to or from the nest is important for the selection of the shortest path.
- For the first time, psychophysical theory has been successfully applied to the pheromone based social behavior of insects.

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ABSTRACT

The emergence of self-organizing behavior in ants has been modeled in various theoretical approaches in the past decades. One model explains experimental observations in which Argentine ants (*Linepithema humile*) selected the shorter of two alternative paths from their nest to a food source (*shortest path experiments*). This model serves as an important example for the emergence of collective behavior and self-organization in biological systems. In addition, it inspired the development of computer algorithms for optimization problems called *ant colony optimization* (ACO). In the model, a *choice function* describing how ants react to different pheromone concentrations is fundamental. However, the parameters of the choice function were not deduced experimentally but freely adapted so that the model fitted the observations of the shortest path experiments. Thus, important knowledge was lacking about crucial model assumptions. A recent study on the Argentine ant provided this information by measuring the response of the ants to varying pheromone concentrations. In said study, the above mentioned choice function was fitted to the experimental data and its parameters were deduced. In addition, a *psychometric function* was fitted to the data and its parameters deduced. Based on these findings, it is possible to test the shortest path model by applying realistic parameter values. Here we present the results of such tests using Monte Carlo simulations of shortest path experiments with Argentine ants. We compare the choice function and the psychometric function, both with parameter values deduced from the above-mentioned experiments. Our results show that by applying the psychometric function, the shortest path experiments can be explained satisfactorily by the model. The study represents the first example of how psychophysical theory can be used to understand and model collective foraging behavior of ants based on trail pheromones. These findings may be important for other models of pheromone guided ant behavior and might inspire improved ACO algorithms.

1. Introduction

1.1. Background

Pheromones play an important role in the emergence of collective social behavior in ants (Hölldobler and Wilson, 1990 p. 227). Importantly, it has been shown that ants, confronted with a binary choice of

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trails of different pheromone concentrations, prefer the trail with the higher concentration. Furthermore, trail following fidelity increases with pheromone concentrations (Choe et al., 2012; Hangartner, 1969; Van Vorhis Key and Baker, 1982). This resembles a communication system, which has the potential to transmit continuous information about different states of the environment.

1.2. Models of ant behavior

The information content of continuous pheromone concentration levels is a central component in models of self-organizing behavior of ant colonies, for example the way in which Argentine ants (*Linepithema humile*) are able to find the shorter of two alternative paths between their nest and a food source and in case of equal path lengths, they collectively select only one of the two paths (Deneubourg et al., 1990; Goss et al., 1989). In the following, we refer to these experiments for simplicity as *shortest path experiments*. This model had great influence by serving as an important example of collective behavior and self-organization of biological systems (Camazine et al., 2001) and inspired the development of optimizing processes called *ant colony optimization* (ACO) in the field of bionics and informatics (Dorigo and Stützle, 2004; Dorigo et al., 1996). Using a similar model, it was shown that the ability of ants to exploit the best quality food source in the environment depends on pheromone concentrations deposited on the trails (Beckers et al., 1992, 1993). The above-mentioned models make use of the same or a slightly modified choice function to describe the stochastic behavior of the ants. We refer to this class of models as the *Deneubourg model* and to the choice function as the *Deneubourg choice function* (DCF) (see Section 2.1 Deneubourg model). The DCF is not only used by ACO and the above mentioned models, but also in other models of ant behavior, for instance in explaining the influence of noise (Dussutour et al., 2009a), the path efficiency in artificial networks (Vittori et al., 2006), the symmetry breaking in foraging behavior (Lanan et al., 2012), the role of multiple pheromones (Dussutour et al., 2009b) and foraging in dynamic environments (Bandeira de Melo and Araújo, 2011; Ramsch et al., 2012).

According to the Deneubourg model, ants decide between two trails at a bifurcation in a probabilistic manner, which depends on the ratio of pheromone concentrations and is described by a choice function. Monte Carlo simulations of the shortest path experiments based on the Deneubourg model produced results similar to experiments conducted with real Argentine ants (Deneubourg et al., 1990; Goss et al., 1989). However, the function parameters were freely adapted to fit the results of the shortest path experiments, since experimental evidence on exact reaction of Argentine ants to different pheromone concentration was rare. In later experiments, Perna et al. (2012) and Vittori et al. (2006) deduced the parameters of the DCF for *L. humile* experimentally and found different values for the function parameters, especially for the exponent. They did not measure pheromone concentrations directly but assumed that the pheromone concentration at a certain point is proportional to the number of ants that had passed that point before. To our knowledge, the parameters of the DCF have never been deduced experimentally based on controlled pheromone concentrations, despite the fact that they are used by many models. Thus, crucial model assumptions have not been tested. A previous study attempted to fill this gap in knowledge (von Thienen et al., 2014) by measuring the response of Argentine ants to varying pheromone concentrations at a bifurcation by using gland extract as well as synthetic pheromone. In the same study, the DCF as well as the *psychometric function* (see Section 2.2 Psychophysical theory) were fitted to the experimental data and their parameters had been deduced. A major finding was that the amount of nonlinearity proposed by the Deneubourg model was much lower than expected and that the response to different pheromone concentrations follows Weber's law (see Section 2.2 Psychophysical theory).

1.3. Aim of this study

In the study presented here, we used the previously deduced parameters for computer simulations of shortest path experiments. Thereby, the data from the previous experimental study allowed, for the first time, computer simulations based on realistic model parameter values, so as to verify the Deneubourg model and the underlying mathematical functions. Thus, based on empirical data, we were able to verify a model of ant behavior that serves as an important example for collective behavior and self-organization in biological systems (Camazine et al., 2001). Here we present and compare the results of these computer simulations and discuss their implications for the understanding of collective ant behavior.

2. The models

An understanding of the Deneubourg model and psychophysical theory are essential for the comprehension of this article. Here, we provide a short introduction into these concepts.

2.1. Deneubourg model

The Deneubourg model was developed to explain important aspects of the collective ant behavior that are based on pheromones (Deneubourg et al., 1990; Goss et al., 1989). The model is based on the finding that ants encode information about the environment by dropping varying amounts of pheromones on their trails and that this information is used by other individuals for directional choices (Wilson, 1962). The model was able to partly explain experiments in which ants have the choice between alternative paths on their way from the nest to the food and back (see Fig. 1) (Aron et al., 1989; Deneubourg et al., 1990; Goss et al., 1989). In such an experiment, a bridge with two branches was placed between the ants' nest and a food source. After an exploration phase, the ants discovered the food and started foraging. Later, the majority of ants preferred one of the two alternative paths. Experimental repetition showed that the path selected in the majority of experiments depended on the difference in length between both paths. If the paths were of equal length, the choice was either left or right with equal probability (see Fig. 2B). If one path was shorter than the other, the shorter path was selected by most of the ants in most of the experiments (see Fig. 2A). Such effects in the foraging behavior of insects have been referred to as symmetry breaking (De Vries and Biesmeijer, 2002; Lanan et al., 2012) and can be seen in the asymmetric distribution along the *x*-axis in Fig. 2A and

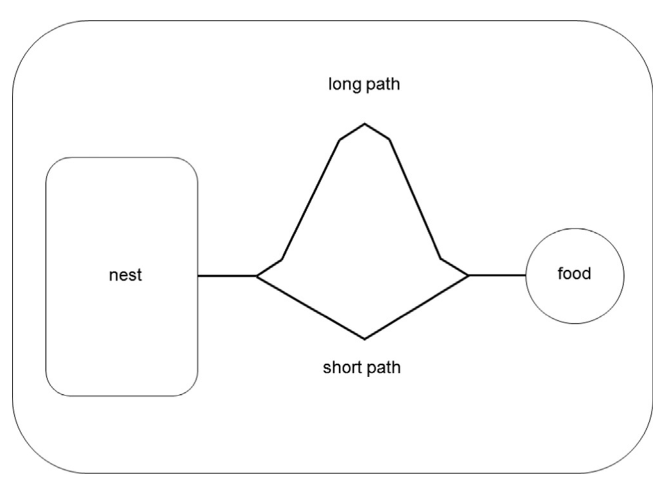

Fig. 1. Schematic experimental setup of the shortest path experiments. In the majority of experiments, most of the ants took the short path between nest and food. Modified from Goss et al. (1989).