Original Research Article

Lévy-like movements in Japanese carpenter ants: Experimental and theoretical approaches

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ABSTRACT

We conducted movement analysis using ant experiments and simulation models. In our experiments, Japanese carpenter ants showed Lévy-like movements when they were exposed to a bowl-shaped test container filled with other foragers. We also developed a one-dimensional multi-agent random walk algorithm. In our algorithm, agents interact with each other and change their probabilities of movements by locally anticipating other agents' moving directions. Agents also modulate those probabilities on the basis of local information, thereby producing fluctuations in averaged local directional information. We were able to induce agents in our model to achieve Lévy-like movements. We also found that an agent occasionally moved or stayed together with another particular agent for a substantial duration in both experiments and simulations.

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1. Introduction

It is very important for many animals to achieve a balance between resource exploitation and exploration in order to find new profits while maintaining reliable food supplies. Specifically with respect to arthropods, the issue of exploitation versus exploration has been discussed for a range of species (Mailleux et al., 2000; Jeanson et al., 2004a; Detrain and Deneubourg, 2006). For example, social spiders produce silk threads that are followed by others. Silk highways are formed by this silk-laying behaviour (Jeanson et al., 2004a). Although navigation is important to all insects, social insects are unique in that exploitation and exploration emerge as a function of the collective behavior of a group. Many ant species, for example, use pheromones; other use tandem running for their navigations when scouts or recruiters find profits (Hölldobler and Wilson, 1990). If followers simply obey scouts or recruiters, they would not be able to find food or potential nesting sites and would thereby become specialized in exploitation, although caste differentiation, with some ants specialized as explorers (the leaders) and some ants specialized as exploiters (the followers) is not entirely implausible (Jackson and Ratnieks, 2006). External noise is known to play a role in new location exploration while specific known locations are being exploited (Hölldobler and Wilson, 1990; Sumpter and Beekman, 2003; Marshall et al., 2006;

Dussutour et al., 2006). Without external noise, how do ants achieve the necessary flexible balance using the noise that they produce? Ants appear to modulate their behaviours actively depending on their circumstances or through interactions with their nest mates (Czaczkes et al., 2013, 2015). These modulations at the individual level may contribute to achieving profits at the colony level (Czaczkes, 2014). Therefore, flexible behaviours may arise from the noise produced by the agents themselves.

Ants appear to use several navigation systems to orient themselves to their nest of feeders (Wehner et al., 2006; Cheng, 2012). However, in the absence of navigation cues, many ants exhibit movements consistent with a random walk. Therefore, environmental cues and/or cues from other local agents must alter an individual's movement rules such that the colony as a whole can capitalize on information about nest and feeder locations. It has been recently shown, for example, that garden ants, *Lasius niger*, can anticipate surrounding spaces using other local agents, resulting in the production of global patterns (Sakiyama and Gunji, 2013a). Despite these recent findings, the more general question of how local agent interactions scale-up to influence global search and recruitment strategies and how this optimizes colony performance remains open. In this paper, we study the question of how agent-agent interactions govern foraging strategies by comparing experiments using Japanese carpenter ants.

A primary theme of random walk problems is how to achieve Lévy-like movements without assuming power-law-tailed distributions because animals show different movement properties depending on environmental contexts, a primary theme of animal

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movement analysis is understanding how local interactions, either with the environment or with each other, manifest as global movement characteristics. In the case of animals that move according to a random walk, this often means understanding what local movement rules yield Lévy -like walks versus Brownian motion (Viswanathan et al., 2008; Reynolds, 2010; Reynolds et al., 2013; Sakiyama and Gunji, 2013b; Sakiyama and Gunji, 2014). For example, they might show Lévy walking on one occasion and Brownian walking on another (Humphries et al., 2012; Sueur et al., 2011; Sims et al., 2012; López-López et al., 2013).

In a Lévy walk, agents show power-law-distributed step lengths (l), as described by the following equation:

$$P(l) \sim l^{-\mu}, \quad 1 < \mu < 3,$$

resulting in long-range exploration and effective searching for agents when desirable locations are scarce or far from their current positions (Boyer and Larralde, 2005; Santos et al., 2007; Kareiva and Shigesada, 1983; Viswanathan et al., 2001, 2005; Bartumeus et al., 2002, 2005, 2008; Bartumeus and Levin, 2008; Faustino et al., 2007; Palyulina et al., 2014). Agents can effectively perform a Lévy walk search because individual agents can search stably in both small regions and distant areas (Viswanathan et al., 2008); therefore, many researchers focus on whether actual animals follow a Lévy walk. This searching pattern might also contribute to a balance between exploitation (near-region searching) and exploration (distant-area searching).

Isolated desert ants are known to show Brownian or composite Brownian walking (Schultheiss and Cheng, 2011, 2013; Schultheiss et al., 2013; Narendra et al., 2008; Reynolds et al., 2014). We conducted experiments using Japanese carpenter ants and examined the possible emergence of Lévy-like movements while walking with conspecifics, as compared with isolated movements. We also conducted simulation analysis, examining whether power-law-tailed properties could be achieved through interactions among Brownian walkers. We developed a random walk model that occasionally produces long step lengths. Agents in our model change probabilities of movements left and right by anticipating other local agents' moving directions. Thus, agents can increase the probability of going in a certain direction (Sakiyama and Gunji, 2015). However, agents in our model are random walkers. Therefore, they do not know whether major direction of other local agents leads to profits or not. Consequently, we introduced a modulation effect in which agents modulate their probabilities of movements left and right depending on the number of other local agents. If the number of other local agents is beyond a certain value, the agent increases the probability of moving in major direction of other local agents. In this paper, we examine how this effect could contribute to obtaining power-law-tailed step lengths. First, we describe experimental and phenomenological results in characteristic movements of swarm ants. Second, we propose a multi-agent model and discuss these emergent properties of Japanese ants.

2. Materials and methods

2.1. Experimental materials

We used Japanese carpenter Ants, *Camponotus japonicus*, which are known to use tandem running rather than pheromones for navigation. Two colonies were used. Each colony included 40–100 workers collected on the campus of Kobe University. We captured workers as they were leaving their nests and starting their foraging. We housed them in plastic boxes ($62.5 \times 43.5 \times 32.0 \text{ cm}^3$ high) wherein a smaller plastic box covered by a red plastic sheet was

introduced for their nests. Honeydew solutions were provided regularly, and fresh water was always available. We applied talcum powder on the walls to prevent workers from escaping. The colonies were maintained at room temperature ($21 \pm 2 \,^\circ\text{C}$) and regularly moistened. One colony was used for both swarm- and single-condition tests. The other colony was used only for the swarm-condition test.

3. Experimental methods

A cylindrical chamber (80 cm diameter, 57 cm height) was set in a square-shaped frame support (Fig. 1). The chamber was covered with a wooden lid ($90 \times 90 \text{ cm}^2$). Three LED light bulbs (LDA6D-H-E17, 6.1 W) were symmetrically set inside the cover with a hole at its centre through which a camera (HDC-TM700, Panasonic) could be inserted. Ants were starved for 3–4 days before each trial. An acrylic bowl (approximately 27 cm diameter) was introduced in the middle of the chamber to be used as a test field.

We used a bowl as a test field because when ants walked with conspecifics on a restricted flat field, they occasionally overlapped or stopped together for a while around corners. This behaviour was not observed in the case of their isolated movements. In addition, we needed to obtain step lengths showing both short and long values within restricted fields. A bowl is essentially a 1D system with periodic boundaries, which approximates an infinite system because there are no hard boundaries. Therefore, by using the described arena, we could obtain reliable step length values by defining step lengths as lengths along one dimension between consecutive turns. In our experimental situation, no walker could obtain any visual information. Also, no walker experienced this field before any test trials. In such a novel circumstance, we would like to evaluate what properties would emerge if each walker was allowed to contact its nest mates. To achieve continuous contact of each agent with other agents, we used a closed field and restricted agents to movement in that field. Although actual measurable distances in that field are limited, distances traversed by each agent might not necessarily be limited because they would be unable to use any visual information or information regarding distances (Sakuma, 2002). Though some readers might wonder whether ants would suddenly be exposed to an unfamiliar area, such a situation is not likely to be extremely odd, especially for ants such as Japanese carpenter ants, whose dominant navigation method involves visual cues rather than pheromones. In this sense, our experimental situation would not be excessively different from natural conditions, even though it would not perfectly mimic ant nature. In addition, they might show some behaviour different from their natural foraging behaviour as they were suddenly exposed to an uncertain area. However, in such a situation, we estimated how the motion of agents would be influenced by
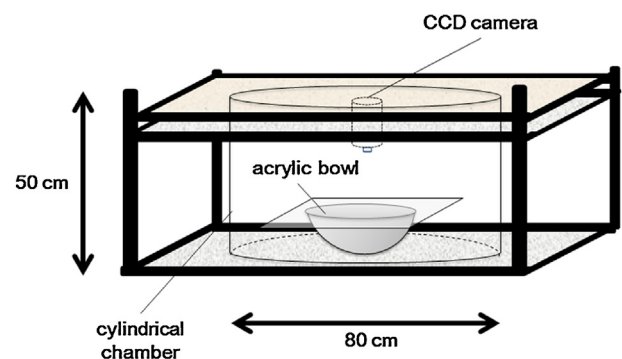

Fig. 1. Experimental setup. An acrylic bowl serving as a test field is introduced into the experimental chamber, which is supported by frames. The experimental chamber is equipped to prevent visual surroundings from influencing ants' behaviours.