

# CORRELATED MOTION OF WEAVER ANTS: ALONE AND IN PAIRS



A Thesis Submitted in Partial Fulfillment of the requirements for the  
Degree of Master of Science in Physics  
Suranaree University of Technology  
Academic Year 2022

การเคลื่อนที่ที่สัมพันธ์กันของมดแดงแบบเดี่ยวและแบบคู่



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วิทยานิพนธ์นี้เป็นส่วนหนึ่งของการศึกษาตามหลักสูตรปริญญาวิทยาศาสตรมหาบัณฑิต

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ปีการศึกษา 2565

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Suranaree University of Technology has approved this thesis submitted in partial fulfillment of the requirements for a Master's Degree.

Thesis Examining Committee



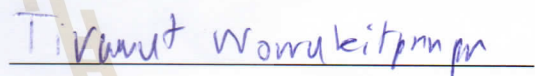
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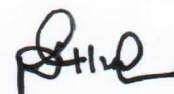
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ปัญญาพงศ์ ไพศาลพันธุ์ : การเคลื่อนที่ที่สัมพันธ์กันของมดแดงแบบเดี่ยวและแบบคู่  
(CORRELATED MOTION OF WEAVER ANTS: ALONE AND IN PAIRS) อาจารย์ที่  
ปรึกษา : ผู้ช่วยศาสตราจารย์ ดร.ไมเคิล เอฟสมิธ, 43 หน้า.

คำสำคัญ: มดแดง, การสื่อสาร, เชิงปริมาณ, ความสัมพันธ์, ผู้นำผู้ตาม

เนื่องจากมดแดงสายพันธุ์ *Oecophylla smaragdina* มีพฤติกรรมที่โดดเด่นในด้านการ  
ทำงานร่วมกันซึ่งเกิดจากการสื่อสารกันจากมดแต่ละตัว พบได้ทั่วไปในมหาวิทยาลัยเทคโนโลยีสุรนารี  
เราใช้กล้องวิดีโอความเร็วสูงจับภาพและติดตามการเคลื่อนที่ของมดแบบเดี่ยว และแบบคู่ ในพื้นที่  
จำกัดบริเวณขนาด  $30 \times 30$  ซม<sup>2</sup> โดยมีสารผสมจากตะไคร้ซึ่งเป็นสารที่มดไม่ชอบทาอยู่ตรงกลางใน  
พื้นที่นี้ การศึกษาการเคลื่อนที่ของมดซึ่งเป็นผลจากการมีปฏิสัมพันธ์กันและอาจเป็นพื้นฐานสำคัญที่  
ทำให้มดแดงสายพันธุ์นี้สามารถทำงานร่วมกันให้บรรลุเป้าหมายต่าง ๆ ได้ การได้วิเคราะห์และ  
นำเสนอคำอธิบายเกี่ยวกับการเคลื่อนที่นี้ทั้งเชิงคุณภาพและเชิงปริมาณ โดยใช้โปรแกรมคอมพิวเตอร์  
วิเคราะห์หลักฐานความสัมพันธ์เชิงปริมาณผ่านความน่าจะเป็นที่มดหนึ่งตัวผ่านจุด ๆ หนึ่งในเวลา  
หนึ่ง และกลุ่มมดของมันผ่านมาจุดนี้ในเวลาต่อมา ผลการทดลองพบว่ากลุ่มมดมีความสัมพันธ์กันมาก  
กล่าวคือ มดมีการปฏิสัมพันธ์และโน้มน้าวการเคลื่อนที่ของกันและกัน อย่างไรก็ตาม มดแต่ละคู่ไม่ได้  
แสดงภาวะความเป็นผู้นำผู้ตาม แต่ละตัวก็มีแนวโน้มที่จะเดินตามกัน ซึ่งอาจมีข้อยกเว้นเดียวที่เป็นไป  
ได้ของความเสมอภาคนี้เกิดขึ้นเมื่อมีสารผสมจากตะไคร้อยู่ ผู้นำซึ่งรับรู้ถึงสารผสมนี้อาจบอกข้อมูลคู่  
ของมัน

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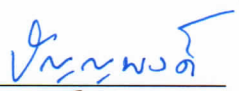
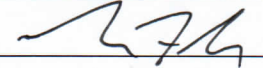
ลายมือชื่ออาจารย์ที่ปรึกษา

PANYAPHONG PAISANPAN : CORRELATED MOTION OF WEAVER ANTS: ALONE AND IN PAIRS. THESIS ADVISOR : ASST. PROF. MICHAEL F. SMITH, Ph.D. 43 PP.

Keyword: weaver ants, communication, quantitative, correlation, leadership

Weaver ants (*Oecophylla smaragdina*) display rich, highly-organized, cooperative behavior; they are also commonly found on SUT campus. We trapped weaver ants and tracked their motion, alone or in pairs, using a high-speed camera. In some experimental trials, we observed the ants moving freely on a square, 30 cm length ceramic floor tile while in other trials we coated a central stripe of this tile with a mild chemical repellent. The goal was to try to understand how the motion of one ant was influenced by its interaction with another, which could provide basic information about how a network of weaver ants is able to communicate so effectively that it can achieve complex goals as a collective. Analyzing their motion quantitatively, particularly measuring and interpreting a correlation function giving the probability that an ant arrives at a given location within the arena a certain time after its partner occupied the same location. In this way, finding that the motion of partnered weaver ants was highly correlated – they interacted frequently and influenced each other’s motion – but that this correlation is symmetric: neither ant takes a leadership role but rather each is as likely to follow the other. The only possible exception to this equitable balance of power occurs when the chemical repellent is present: a leader, perhaps having more knowledge of the local hazards, can emerge. We present a detailed description of the motion of single and paired ants in a simple, unfamiliar, featureless (albeit artificial) environment and give qualitative and quantitative analyses.

School of Physics  
Academic Year 2022

Student’s Signature   
Advisor’s Signature 



## ACKNOWLEDGEMENTS

This thesis could not be accomplished without much support from the following people. Firstly, I would like to thank Dr.Sukrit Suksombat for giving me the opportunity to do experiments with planaria since the Bachelor Degree. Because of that I feel enjoy and love Biophysics. He introduced me to Asst. Prof. Dr.Michael F.Smith who have been my advisor ever since, and I am very grateful. The powerhouse of our little Biophysics group here at School of Physics, Suranaree University of Technology. Without them, it would not be possible to even inspire this research. They enlightened, encouraged, and gave me everything: knowledge, lectures, advice to do experiments and to do programming and also guided me to think systematically and critically. I have learned so much from them. I sincerely appreciated.

I would like to thank School of Physics, Suranaree University of Technology, for the laboratory and facilities. Also, all lecturers and staff members, especially, P'Noey, P'Khae, and P'Jang. They helped me so much about the paper stuff.

I thank to the Royal Thai Government scholarship through Development and Promotion of Science and Technology Talents Project (DPST) for the financial support.

Last but not least, I would like to thank to my family, friends, and senior colleagues for their love, encouragement, and support throughout the process and for motivating me to complete my study.

Panyaphong Paisanpan

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## LIST OF ABBREVIATIONS

COM	Center of Mass
2D	2 Dimension
HD	High Definition
SC	Single ant in Clean arena
SR	Single ant in Repellent arena
PC	ant Pair in Clean arena
PR	ant Pair in Repellent arena
RGB	Red Green Blue
LF	Leader-Follower



มหาวิทยาลัยเทคโนโลยีสุรนารี

# CHAPTER I

## INTRODUCTION

### 1.1 Ants in general

Ants are everywhere, and one cannot help notice that their group behavior is highly organized: members work together to achieve certain goals. The organized motion of this complex system, which is ultimately made possible by communication between individuals, has attracted scientific interest for centuries. When humans cooperate on a large scale they are often following directives from a leader, but this does not appear to be the case for ant colonies. A longstanding question has been: how do ants get anything done without anyone in charge? An ant colony consists of one or more reproductive females, called “queens”, who lay eggs. All the rest of the ants are daughters of the queen, including the ones you see walking around, which are sterile female “workers”. With all its members related, it is the colony, not the individual ant that has achieved evolutionary fitness. An individual ant is analogous to a cell with the super organism, so the question posed above can also be asked about the cells in a human embryo. All cells are formed from one or two parent cells, so they all have the same genes. By what process is organized development, such that one cell becomes lung, and another becomes skin, achieved? With this in mind, researchers have been doing experiments with ants, of many different species. They are motivated by the possibility that a better understanding of ant organization could help us determine how our own bodies are formed or understand other systems that operate with no central control. Perhaps the ant colony holds more secrets. Ant researchers hope that their works will be applicable for organizing robot colonies, and even solve some of our society’s problems.



## 1.2 Ant-collective behaviors

Ant colonies are self-organized. This means they can produce complex, purposeful structures and demonstrate collective behavior. The colonies have no apparent central control so the collective behaviors must arise from simple interaction of individuals. The modes of communication are very diverse. They clearly communicate using their antennae, and possibly other body parts. These communications are based on touch (direct communication), the sight of body language, as well as sound and scent. The scents, particularly, are chemicals produced by the ants themselves. They are called pheromones and are believed to convey messages of alarm and information to help find resources. For example, one ant can lay a trail of pheromones that marks a path on the ground between the nest and a food source. Others can follow this path. This general phenomenon has been termed “stigmergy”; where an agent leaves a trace in the environment waiting for the same or other agents to perform the next action, was proposed by Pierre-Paul Grassé (Grassé, 1959). We can imagine that, if each ant participated in such a communication network, the colony could function effectively as a whole without needing top-down messages from any leadership. Ant colonies are not the only complex system that function without central control. Thousands of starlings that wheels in the sky. Brains, too, have no chain of command. They rely on interaction networks among neurons that allows you to read this sentence (Gordon, 2016).

Simple interactions are the key to all complex biological systems. Local interactions among the parts produce coordinated behavior of the whole. This is our picture of the effective ant colony. The responses and interactions of individual ants add up to colony behavior which is dynamic, always changing because the world of colony is always changing (Gordon, 2010).

But how, exactly, do ant colonies organize their work using simple interactions? In the case of finding food – like the ants you see walking on your kitchen counter, we

have some understanding. Successful scouts lay a chemical trail as they return to the nest with food. Some foragers remain in the nest until they have met a sufficient number of such scouts. Once they have, they set out along the pheromone trail (Hölldobler and Wilson, 1998). These followers add their own pheromones, amplifying the trail. In this way, the efforts of the colony are focused on the most important targets.

However, they manage it, the efficacy of ant collective behavior in certain species is remarkable. When the route of a marching troupe is blocked, say by water or by a gap between tree and branches, some the ants are capable of building bridges using their own bodies. The troupe can cross the bridge built of their comrades and the flow of the colony proceeds, see Figure 1.1 (Reid et al., 2015). Even more remarkably, ants can build nests in trees by bending and gluing together broad leaves – the manipulation of each leaf requiring the effort of hundreds of individuals working in concert. These projects require communication and coordination among large numbers of individuals spread across large distances: a construction crew of hundreds or thousands of ants must plan, and combine their strength (Sakiyama, 2017; Vernerey et al., 2018). Perhaps the most famous example of such collective efforts is performed by the fire ants, *Solenopsis invicta*: living rafts built with their own bodies that they use to float the entire colony and survive floods. These boats can voyage for weeks until a new home is found (Mlot et al., 2011), with various tricks used to keep the entire colony alive: the passengers, the crew, and the very boat itself! Another example of collective ant behavior, one that is less spectacular but more directly related to our own work, is illustrated by ants able to find the shortest possible path to a food source, even when confronted by obstacles and repellents. Each ant chooses its own walking path according to an innate navigational algorithm, but for a large group of ants to effectively locate food together, communication is vital. Perhaps ants that encounter a dead end warn others not to make the same mistake while ants that find a fruitful

path signal others to follow the same route. In any case, an ant must modify its own navigational algorithm in response to information it receives from comrades.

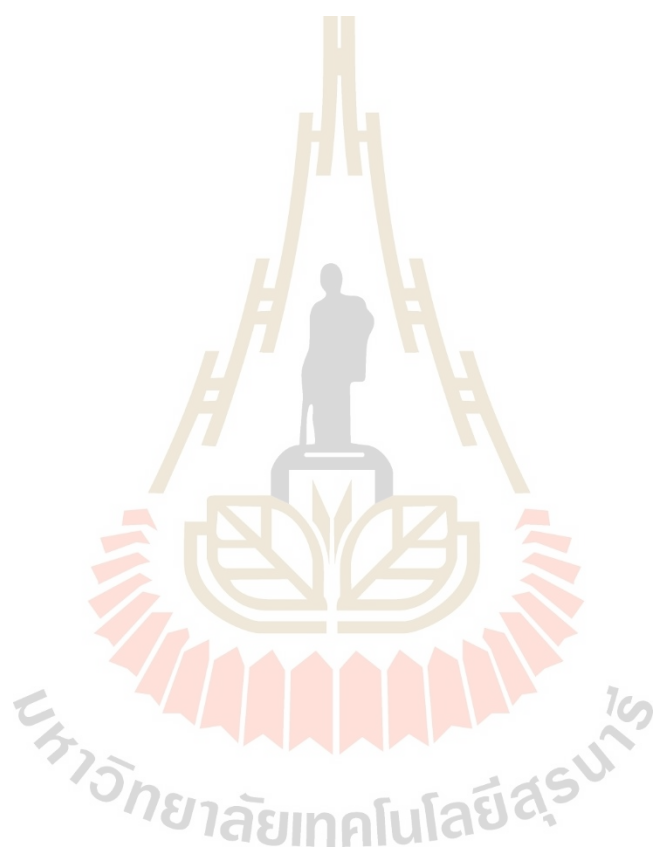


**Figure 1.1** Weaver ants build their living bridge to cross a gap (the figure was obtained from <https://en.wikipedia.org/wiki/Ant>).

### 1.3 Project summary

In this research, we look for quantitative evidence of ant-ant (*Oecophylla smaragdina*) correlations within the navigational patterns of ant individuals. That is, we look for the observable change in the walking pattern of a single ant that occurs because of the presence of a second ant. We want to study quantitative correlations only, because we feel that qualitative characterization of ant behavior would introduce our own subjective judgments, and we want to minimize this. The correlations could arise because of communication between ants: an ant that receives new information from a fellow might modify its future path in light of this information. It could also arise for less interesting reasons, such as ants having to physically pass around each

other. But certainly, an understanding of quantitative ant-ant navigation correlations is potentially a first step in understanding a basic element of their communication.



## CHAPTER II

### LITERATURE REVIEWS

#### 2.1 Weaver ants

The earth is home to over 14,000 species of ants, distributed widely. Some build nests in the ground, in hollow of tree branches, under rocks, in leaves or even in your backyard if you look really closely.

Weaver ants in the genus *Oecophylla* consist of two extant species – *O. smaragdina*, which is distributed throughout tropical Asia, Australia and some Pacific islands and *O. longinoda* of tropical Africa (Lokkers, 1986; Hölldobler and Wilson, 1990). They are relatively large, with bodies up to 10 millimeters in length. These weaver ants build leaf nests on their host trees; they bend huge tree leaves (20 cm in diameter) and glue edges together with silk produced from their larvae to construct a spherical nest. The ants prefer a sunny habitat, so they make use of whichever tree is suitably located – they have to adapt their construction techniques to the host tree. Thousands of individuals work together (Cole and Jones, 1948; Ogawa et al., 2023). It requires communication over a range of length scales. The mechanisms of communication employed by weaver ants, using pheromones, gestures, and direct contact, are indeed sophisticated and have attracted the longtime interest of biologists. Weaver ants are more often studied with regard to harvesting and farming and utilized directly as a protein and food source. Lately, they also make them an attractive subject for the physicists in term of collective phenomena in complex systems. The effect of communication on ant motion is a topic of interest (Thiwatwananikul et al., 2020; Kamhi et al., 2015; Golden and Hill, 2016).





**Figure 2.1** Weaver ant nest in a tree (the figure was obtained from <https://www.flickr.com/photos/smithandjones/15823865013>).

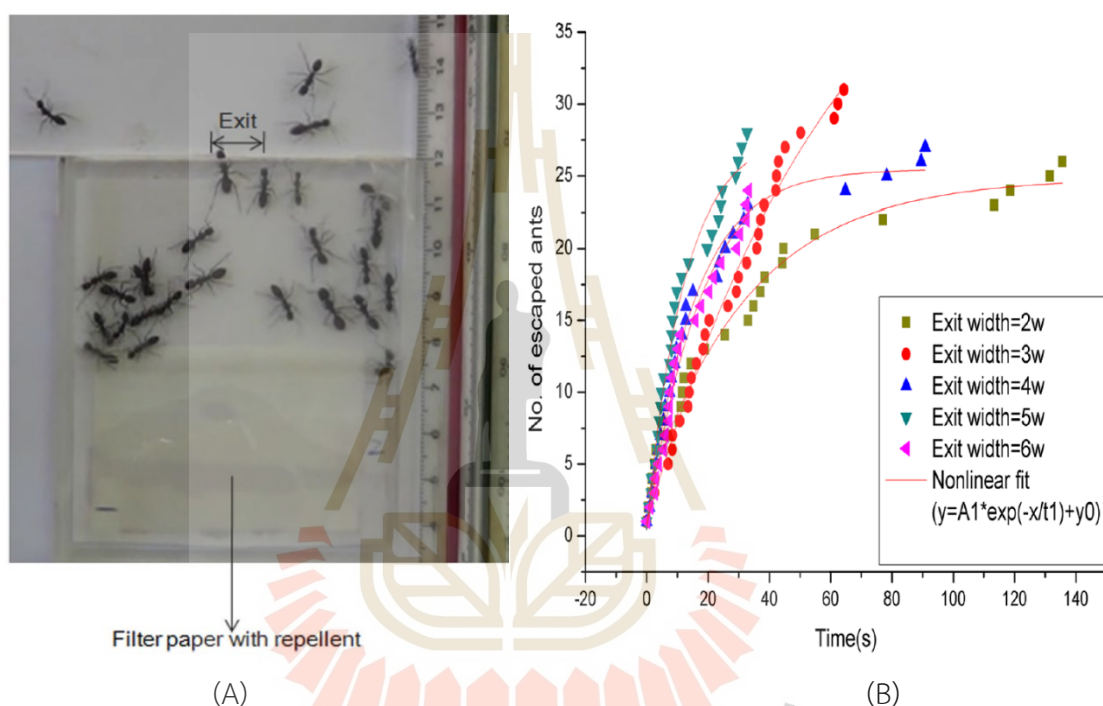
## 2.2 Ant repellent

Colonies are regulated by networks of interaction. Ants must consider both features of their immediate surroundings and the communicating signals of other ants to decide what to do. There has been a lot of work done on the response of ant populations to uncomfortable conditions e.g., chemical irritants and heat. The general finding is that ants make well-organized retreats from such hostile territory.

For example, in one experiment ants were placed into a rectangular room that contained a paper soaked with citronella oil, a natural repellent. The time required for each ant to escape through the single door, with a width that varied between trials, was recorded. In a disorganized escape attempt made by uncorrelated individuals, the inverse of the average escape time would increase linearly with the door width. This is because a crowd would form near the door and the rate of final escape would be



limited by the inefficient flow through the bottleneck of individuals jostling for space. In Figure 2.2, the measured distribution of ant escape time exhibited an exponential decay with time and a weak dependence on door width. The results indicate that ants were not jamming near the exit but rather were using a better strategy (Wang et al., 2015). The comparison to human behavior in comparable situations is humbling, while tragic.



**Figure 2.2** (A) The snapshot from video recording of ants evacuating from a single-exit room. The exit width is 1.0 cm, with citronella oil used as a chemical repellent. (B) Flow rate of escaping ants in the presence of this repellent. The evolution of the number of ants escaping through an exit room size of  $1w = 0.5$  cm and other exit sizes which are  $2w = 1.0$  cm,  $3w = 1.5$  cm,  $4w = 2.0$  cm,  $5w = 2.5$  cm, and  $6w = 3.0$  cm are shown. The solid lines represent results of nonlinear fitting where  $y$  is number of escaping ants and  $x$  is time (Wang et al., 2015).

In another example, Argentine ants, *Camponotus japonicus*, were placed into a two-dimensional chamber connected to an external input voltage that released heat at the bottom plate of the chamber. This was done to study ants' response to a

potentially harmful stimulus. When all ants were in the chamber, the heat source was turned on and the temperature adjusted with five fixed different input voltages, 15V, 20V, 30V, 40V, and 50V, respectively. The results showed that ants did not go directly towards the exit. The density of ants near the exit was low, and jamming or clogging was not observed. The mean evacuation time decreased as the input voltage of the heat source increased. This indicated that ants appropriately assessed the level of danger and evacuated efficiently (Boari et al., 2013).

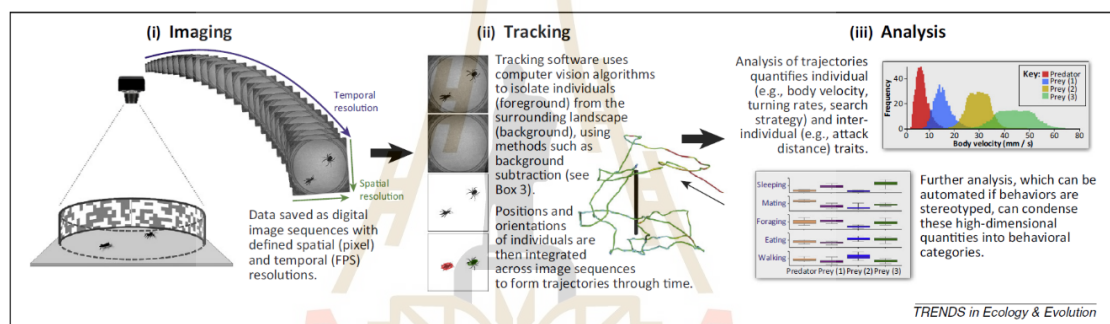
### 2.3 Image-processing in ecosystems

Historically, direct observation by trained scientists was used to quantify the motion of ants and other biosystems. Limitations of this method include the extent and resolution of data and the number of individuals that can be observed simultaneously (Altmann, 1974; Dankert et al., 2009). Attempts to characterize behavior, say by defining distinct phases of motion (such as “resting”, “searching”, “directed movement” etc.) is a natural and common practice used to help organize data into manageable segments. But it requires subjective assessments and risks introducing anthropomorphic assumptions.

Image-based tracking, for example with video, is another method that shows great potential in ecology. This involves digital recording of data. A far greater quantity of events can be amassed and stored, with scientists free to mine this data for quantities beyond those originally considered. Moreover, it is convenient to analyze the results objectively. Even if phases of motion are considered, the phases can be defined quantitatively – i.e., according to measurable parameters of the motion that are out of the hands of the human researchers. (Of course, the conceptual definition of the phases still introduces some subjective judgments.) There are three key areas in ecology that have been widely studied using this technique. First, the kinematics of

animal behavior. Second, collective behavior in animal groups. And third, determinants of social behavior (Dell et al., 2014).

The image-based tracking considered in this work involves three main steps (Figure 2.3): (i) raw data, a sequence of images taken at defined time intervals, is collected; (ii) detection of (ant) individuals is made in each image to create trajectories over time; and (iii) the trajectories are analyzed to understand behavior – at this stage various properties of the motion, which are functions of the trajectories, can be extracted.



**Figure 2.3** Three main steps of image-based tracking. (i) Sequence of images. (ii) Tracking using by computer program from consecutive images through time. (iii) Analysis of trajectories (Dell et al., 2014).

The most basic output from tracking are the coordinates of the center-of-mass (COM) of individuals through time. Tracking is easiest in laboratory-based systems with a simple environment and low numbers of individuals. Monitoring the behavior of individuals as they interact with each other is difficult because organisms often move rapidly when interacting, requiring data with high resolution. In addition, multiple individuals are involved and interactions often involve close physical contact.

This technique is widely used, and we give here one illustrative example. One was the quantitative characterization of the behavior of the freshwater planarian. The method is based on a simple experimental setup, using automated center-of-mass

(COM) tracking. The trajectories were recorded and analyzed to obtain velocity and orientations for behavioral locomotion phenotypes (Talbot and Schötz, 2011).

Since weaver ants display rich social behavior, they make an attractive subject for image-based analysis. Moreover, these ants are readily available in Thailand and their 2D motion is relatively easy to track. We were thus motivated to apply techniques used on other biological systems to these ants. The project aims to study and analyze the position versus time data on weaver ant individuals in simplified environmental conditions.



## CHAPTER III

### MATERIALS AND METHODS

#### 3.1 Experimental design

In this work, we study the motion of weaver ant individuals (*Oecophylla smaragdina*). The patterns of motion are analyzed when an ant is alone in a simple, small arena. Then we introduce a second ant to the same arena and track the motion of both. We measure the quantitative correlations between the position-time data of the two ants and analyze it in search of evidence of ant-ant correlation and the related communication.

We placed a square ceramic floor tile inside a bowl containing a small amount of water, so the top of the tile remained dry but was bounded by water. The tile served as our arena: a 30 cm x 30 cm x 0.6 cm featureless surface surrounded by water channel, a natural barrier that the weaver ants rarely attempted to cross. The arena was located in an unremarkable room. We placed two lamps near the bowl to adjust contrast and shadow of the light in the laboratory room because it is important in video-tracking for our program. A high-resolution video camera: Logitech HD Pro Webcam C920 with a tripod is set up behind the table. The camera is about 45 cm high from the table to cover all the arena area as in Figure 3.1. For all experiments, ants were captured in the wild and transported to the laboratory in a clean plastic container before being gently introduced, alone or in a pair, to the arena where their motion was observed.

We divided experiments into four configurations:

- The experiments with single ants in clean arena (so that the arena is approximately homogeneous). We called this as SC (single ant in clean arena), in Figure 3.2A.
- The experiments with single ants in arena partly coated with repellent. This time, the central rectangular band of the arena was uniformly coated with 1% w/w citronella oil, a natural repellent that is aversive but nonlethal to ants (Wang et al., 2015, 2016). We called this as SR (single ant in repellent arena), in Figure 3.2B.
- The experiments with ant pairs in a clean arena. We called this PC (ant pair in clean arena), in Figure 3.3A.
- The experiments with ant pairs in arena partly coated with repellent. We called this as PR (ant pair in repellent arena), in Figure 3.3B.

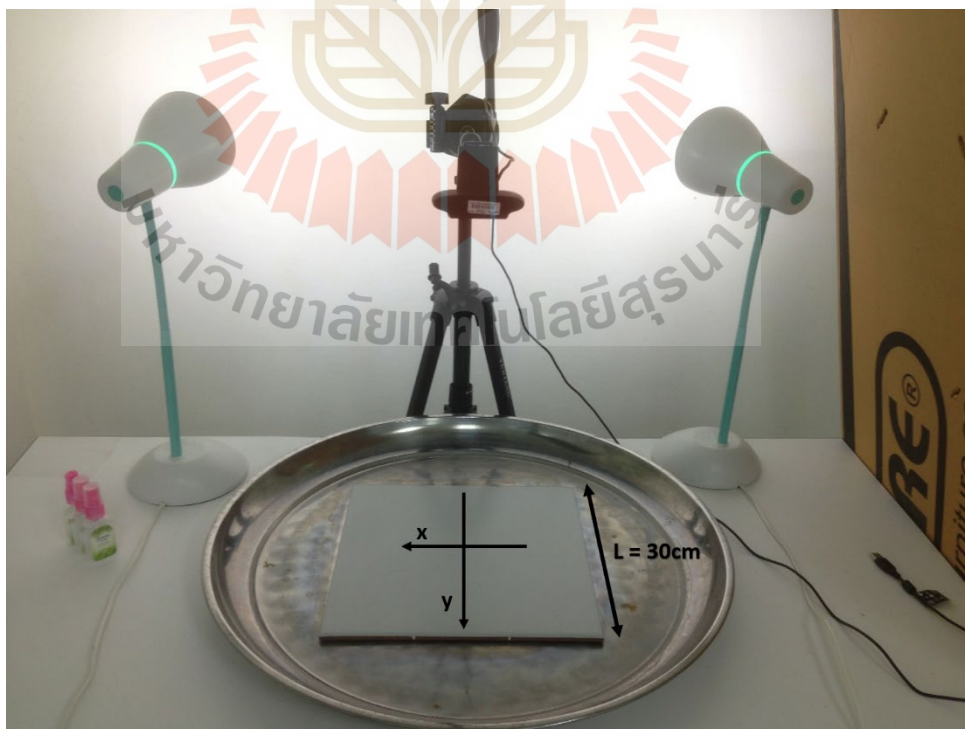
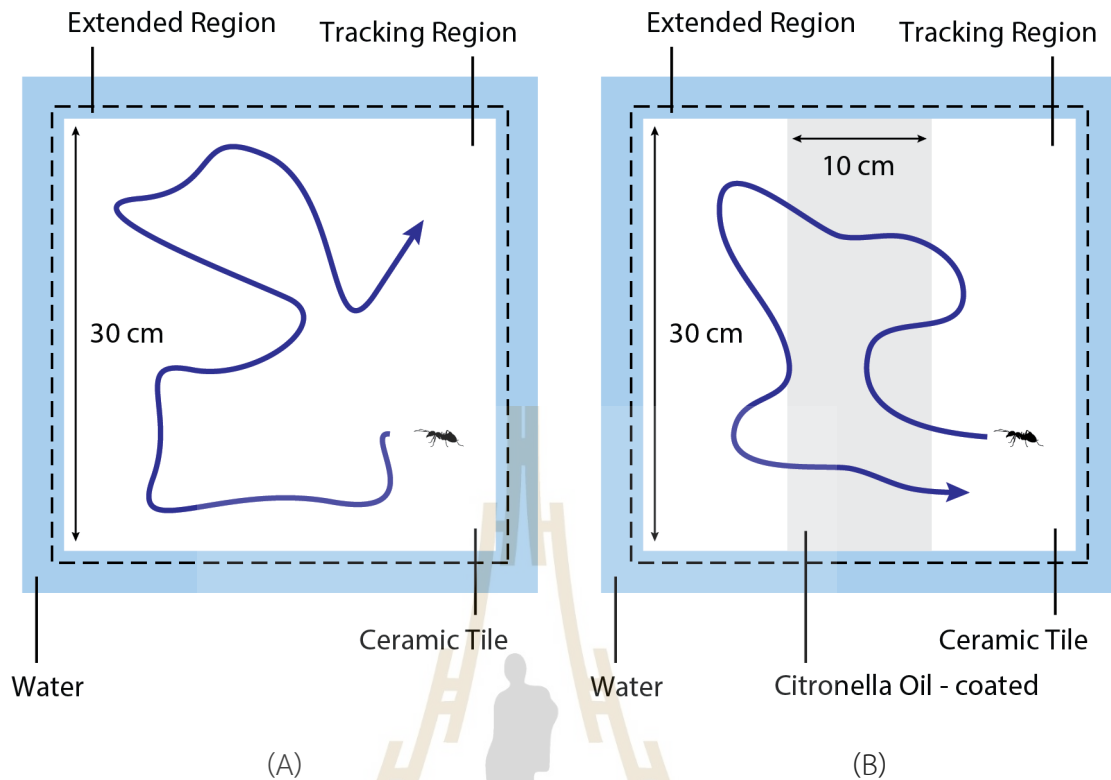


Figure 3.1 A station setup designed to record ant motion.

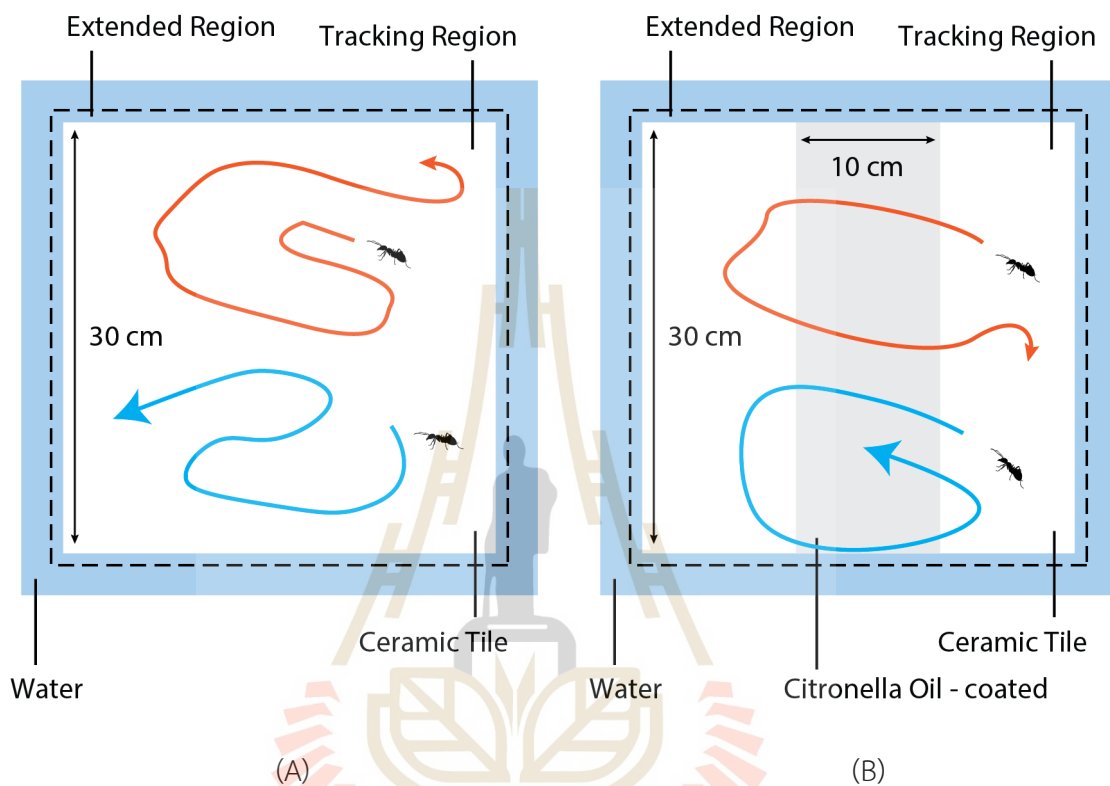




**Figure 3.2** Two schematics of the experimental setup as seen from the top view (the camera view). The clean regions are indicated by white color and the regions coated with citronella oil (a repellent) are indicated by the gray color (in reality, the oil is colorless). (A) The experiments with single ants in clean arena (SC). (B) The experiments with single ants in an arena partly coated with repellent (SR).

The ants were major-workers from *Oecophylla smaragdina*, belonging to one of several colonies, were captured from wooded areas of Suranaree University of Technology, Nakhon Ratchasima, Thailand. When individuals from different colonies were paired, they attacked one another. So all experiments on pairs used two from the same colony. It should also be noted that we used dozen of tiles, nearly indistinguishable from one another. After a tile was used, it was washed in dishwashing soap and water and left to dry before being reused in a different trial. A useful symmetry in the experimental configuration results from the fact that a tile (which appears square-symmetric to first glance) was laid down with a random orientation, i.e.

one of four possible equivalent orientations, so that an average over many trials naturally obeys square symmetry.



**Figure 3.3** Two schematics of the experimental setup seen from top view (the camera view). The clean regions are indicated by white color and the regions coated with citronella oil (a repellent) are indicated by gray color (in reality, the oil is colorless). (A) The experiments with ant pairs in clean arena (PC). (B) The experiments with ant pairs in arena partly coated with repellent (PR).

In each trail, ants were gently released from plastic containers. We opened the lid and placed the plastic container softly onto the arena on the right side of the camera. We waited until the ants all got down on their own onto the arena (to minimize stress from us that may affect ant behavior) and we immediately recorded the ants' movement then quickly removed the plastic container right away from the arena. We recorded videos for 5 minutes in each trial. There was no evident change in

behavior seen over the 5 minutes. Typical ants continued moving throughout the trial. After the recording process was done, we kept the ants in the plastic containers and released all of them to the same colony from which they had been captured.

Note that, previously, we did the experiments in SC and SR configurations as published of (Thiwatwanikul et al., 2020).

### 3.2 Image-based tracking

After the ants' movement was recorded by the high-speed camera, we performed image-based tracking. A video is a sequence of still images. The in-house image processing scripts coded in MATLAB R2018b extracted the position (x and y) of the ants in the video. The image-based tracking works as follows:

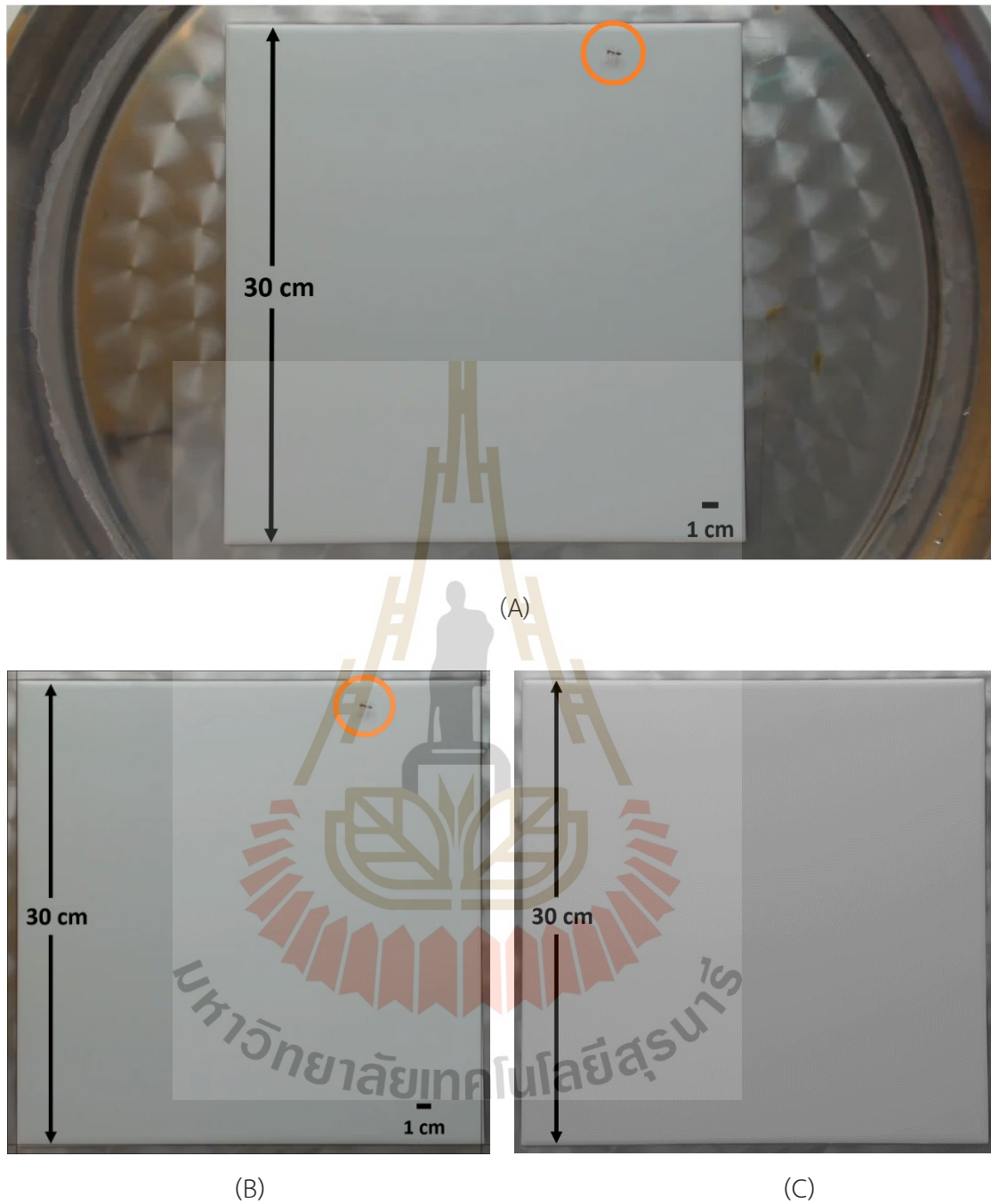
- i. The video is imported to MATLAB R2018b program: we have already written the codes for tracking. Figure 3.4A is an example of still images.
- ii. We choose the region for cropping the coordinates of the arena. Each mathematical point belongs to a square, of finite size, called a pixel: the pixels form a square grid that cover the arena. Sometimes the ant moves near the edge of the arena so that its head is outside the arena but its legs still within it. To allow for this, we increase the region a further 20 pixels at the perimeter, as shown in Figure 3.4B.
- iii. When we have chosen the region, we use the function in MATLAB, which is RGB-to-gray-scale conversion to create an average background in Figure 3.4C. This background is utilized to subtract a sequence of still images frame by frame. So, when we subtracted the still images, we get a sequence of still images but this time we only have just an ant's position as shown in Figure 3.5A.
- iv. Then every still image is converted to black-and-white image and removed noise (as seen below of an ant in Figure 3.5A) by selecting connected area that has fewer area than the threshold we set, in Figure 3.5B.

- v. Finally, every still image is dilated to be got any information such as the center of mass (COM) in x-y coordinate, in Figure 3.5C.

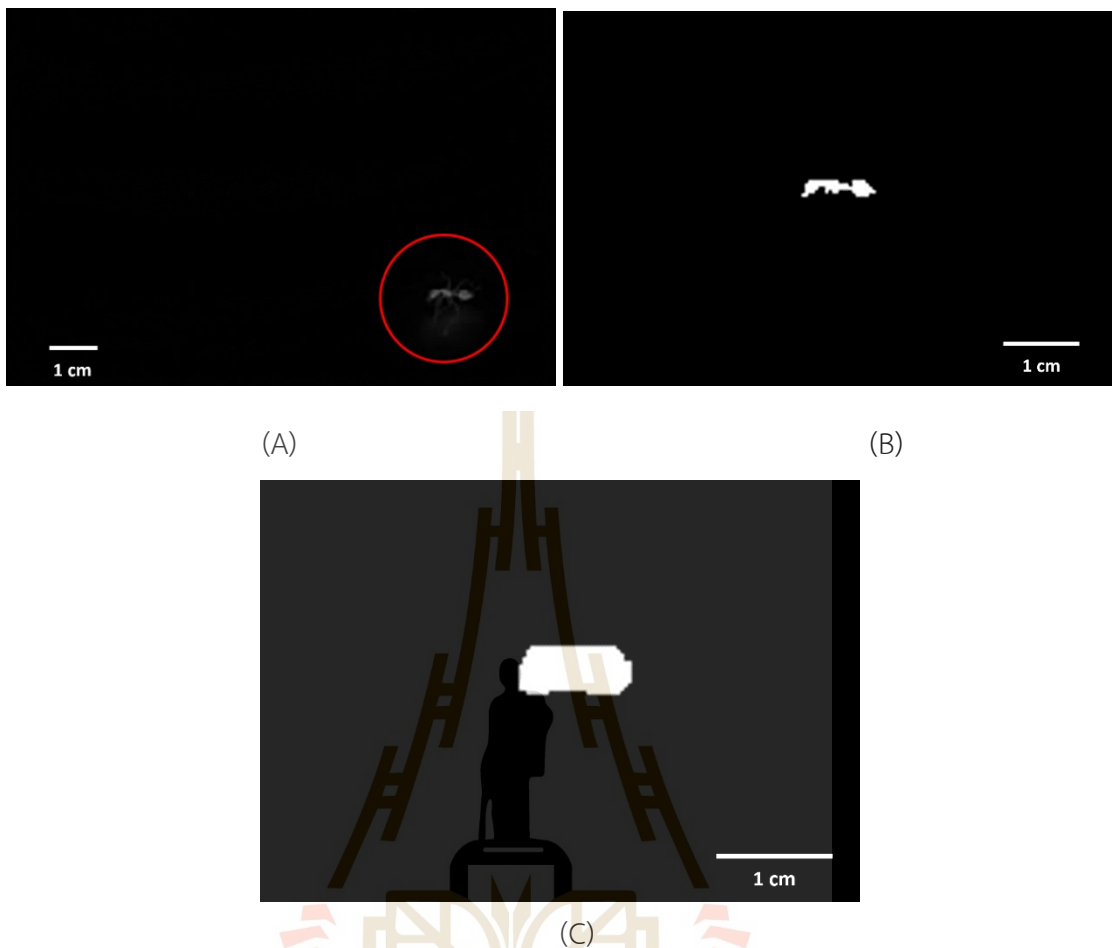
These Figure 3.4 and Figure 3.5 were an example of single-ant tracking (SC and SR configurations). When we tracked the ant pairs, the members of each pair were labeled A and B, arbitrarily. Our scripts can be tracked as many as ten or more of ants at the same time but it was not optimized. That is, there were some problems in labeling ant A and B when a pair had come into close proximity at a particular time. This confused the tracking algorithm, i.e. it sometimes swapped the identities of ants A and B after they had separated. Therefore, we had to re-watch the relevant segment of video after the process was done to verify that the labeling was correct and fix it otherwise (see more information in appendix).

### 3.3 Analysis and theory

Ants' movement was tracked by our in-house scripts coded in MATLAB program. The data consists of position and time measurements. Other parameters or properties were obtained by re-organizing and analyzing  $x(t)$  and  $y(t)$  such as velocity, acceleration, change in velocity, and heat map. Previously, we developed a model of single ant navigation that is analogous to the description of Brownian motion (Thiwatwanikul et al., 2020). In this work we are most concerned with the correlation between the motion of ant pairs.



**Figure 3.4** The image-tracking process using MATLAB R2018b program. (A) An example of original still images from a video file. (B) Cropping coordinates of the arena to be tracked. (C) An average gray-scale background to be subtracted a sequence of still images. Note that, orange circle in (A) and (B) is an actual ant.



**Figure 3.5** (A) A zoom in of a still image after being subtracted from the average background. Inside a red circle is an ant with noise. (B) A zoom in of a still image after being converted to a back-and-white image and with noise removed. (C) A zoom in of a still image (from Figure 3.5B) after being dilated to be got any information such as the center of mass (COM) in x-y coordinate.

We have used a particular function to see the dynamic correlation between ant pairs. Basically, this correlation function describes how variables co-vary with one another on average across space and time.

Suppose an ant has position  $\vec{r}(t) = (x[t], y[t])$  at time  $t$ . We can define a density function for the ant by  $n(x', y', t) = \delta(x' - x[t])\delta(y' - y[t])$ . This function is equal to one if the ant position  $(x[t], y[t])$  falls within the same pixel as a given position  $x', y'$  and is zero otherwise.

Now we define an average of any function of position by

$$\langle f \rangle = \frac{1}{T} \frac{1}{L^2} \int_0^L dx \int_0^L dy \int_0^T dt f(x, y, t)$$

We see that  $\langle n \rangle = \frac{1}{L^2}$ , where  $L$  is arena size.

Now consider two ants, A and B with density functions:  $n_A(x, y, t)$  and  $n_B(x, y, t)$ .

Consider the following average correlation function:

$$G(r_x, r_y, \tau) = \langle n_A(x, y, t) n_B(x + r_x, y + r_y, t + \tau) \rangle$$

Which indicates the probability that ant A is at position  $x, y$  at time  $t$  and ant B is at position  $x + r_x, y + r_y$  at time  $t + \tau$ . This probability is very small, so we consider a finite square neighborhood surrounding point  $x, y$  (around at A), like this:

$$G(d, \tau) = \int_{-\frac{d}{2}}^{\frac{d}{2}} dr_x \int_{-\frac{d}{2}}^{\frac{d}{2}} dr_y \langle n_A(x, y, t) n_B(x + r_x, y + r_y, t + \tau) \rangle$$

Which indicates the probability that ant A is at position  $x, y$  at time  $t$  and ant B is anywhere in the small square near  $x, y$  at time  $t + \tau$ . That is, ant B has a position somewhere in the range between  $x - \frac{d}{2}$  and  $x + \frac{d}{2}$  and between  $y - \frac{d}{2}$  and  $y + \frac{d}{2}$ . Note the asymmetry of the time variable defined this way. If ant A has position  $x, y$  at time  $t$  and ant B arrives in the same neighborhood at time  $t + \tau$  then we get a contribution to the correlation function. For positive values of  $\tau$ , ant A arrived first while for negative  $\tau$  ant A arrived second. So if ant B is following ant A around, then we expect to get large values  $G(d, \tau)$  for  $\tau > 0$ . If A follows B, then we expect to see large  $G(d, \tau)$  at  $\tau < 0$ . The utility of this function is that it characterizes the correlation between ants, which may result from their communication or some other form of their interaction.

### 3.4 The correlation function and ant hierarchy

Consider first the correlation function of two ants that do not interact at all. This is a measurable quantity: we can measure the correlation function for two ants in



*different* arenas, which certainly don't interact. The probability that ant B has a given location is independent of the position of ant A. So, when we measure  $G(d, \tau)$ , we find that it is independent of time  $\tau$ . (Strictly speaking, there is a very weak  $\tau$  dependence that results from the finite size of the data set: when  $\tau$  is large, there are smaller number of data point pairs that fit within the data set.)

Now consider  $G(d, \tau)$  for two interacting ants. When  $\tau$  is large and positive, the quantity reflects any enhanced probability that ant B will visit a region a long time after ant A has left it. (While such a tendency might occur because of long-lived pheromone trails, we do not observe it here.) We expect that a sufficiently long  $\tau$  will erase any memory that ant B had of the whereabouts of ant A. This means we expect that  $G(d, \tau)$ , for large  $\tau$ , should be essentially identical to that measured for independent ants. This is exactly what we see. However, for small positive  $\tau$ , we are studying the tendency for ant B to arrive at a location just after ant A left it. If ant B is following ant A, or if it is drawn to be near to ant A, then we expect the correlation function  $G(d, \tau)$  to be enhanced at small  $\tau$ , i.e., to have a value far larger than it does for independent ants. This observed peak is prominent.

A second important aspect of the correlation function is the information it contains about ant hierarchy. Is one of the two ants leading the other? If ant A is leading ant B then we should see an asymmetry in the correlation function: with  $G(d, \tau)$  for positive  $\tau$  larger than the corresponding value of  $G(d, -\tau)$ . If ant B is leading ant A then the opposite statement should be true. Thus, our data allows us to objectively determine which, if either, ant is dominant over the other.

We use the following procedure in order to best approach the leader/follower dichotomy. For each trial, the labels ant A and ant B are arbitrarily assigned to the two ants. If we averaged  $G(d, \tau)$  over many trials then we would expect to see perfectly even symmetry  $G(d, \tau) = G(d, -\tau)$  simply because there is no difference, on average, between an ant labeled A and an ant labeled B. However, we can identify, after each trial, which of the two ants is the probable leader by comparing the integral of  $G(d, \tau)$

(for a single trial) over positive and negative  $\tau$ . If there is more weight on the positive side, then ant A is the leader  $L$ , while ant B is the follower  $F$ . If there is more weight on the negative side, then ant B is the leader  $L$ , while ant A is the follower  $F$ .

Having relabeled the two ants of each trial as  $L$  and  $F$ , we can again find the average correlation function  $G(d, \tau)$  over all trials. But this time it is the correlation between ants that have meaningful labels  $L$  and  $F$ . Doing it this way, we are guaranteed to have some asymmetry  $G(d, \tau) > G(d, -\tau)$  because we have reordered the data such that the leaders are always associated with the positive  $\tau$ .

Now, if the extent of this asymmetry is pronounced, then we would be tempted to conclude that ants, in the conditions of the experiment, do respect a hierarchy: one of them acts as a leader. On the other hand, if the averaged  $G(d, \tau)$  still demonstrates no significant asymmetry, even though we have given it every reason to do so, then we can more strongly conclude that there is no leader among the paired ants. That is, if the trial-averaged correlation function  $G(d, \tau)$  between ant  $L$  and ant  $F$  appears to be approximately symmetric, then our results would suggest an equitable balance of power between the paired ants.

## CHAPTER IV

### RESULTS

#### 4.1 Experimental results

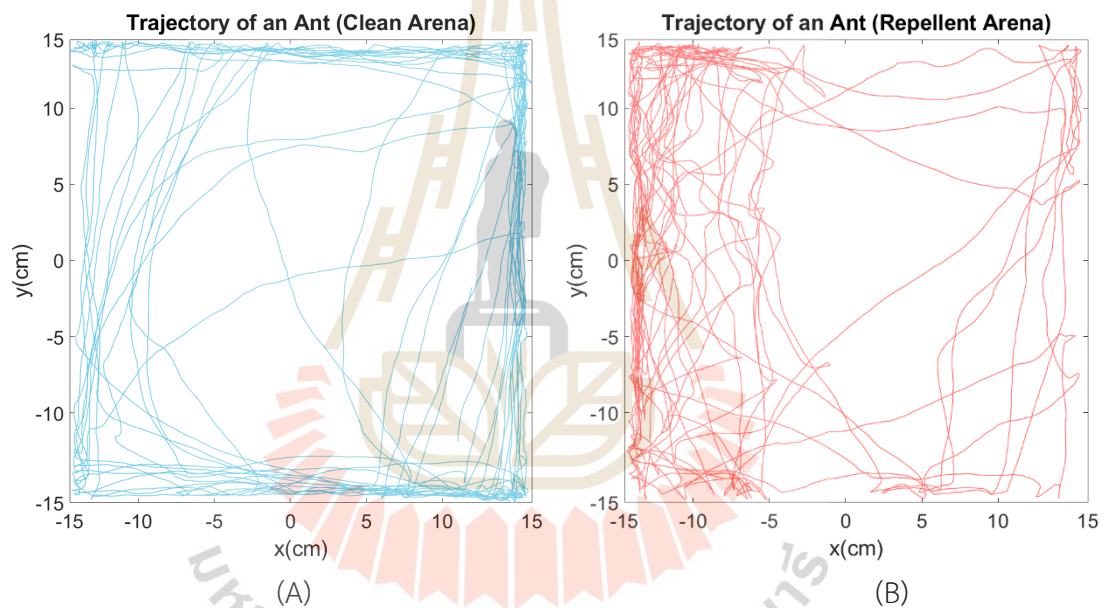
Recall from the previous chapter that trials were conducted with single ants in clean arenas (denoted SC) and single ants in arenas that had a central stripe coated with a chemical repellent (SR) as well as pairs of ants in a clean arena (PC) and similarly coted arena (PR). The number of the trials done for the SC, SR, PC, and PR configurations were 59, 68, 12 (pairs), and 24 (pairs), respectively. No ant participated in more than one trial, and the ceramic tile used for the arena was changed after each trial.

##### 4.1.1 Qualitative observations

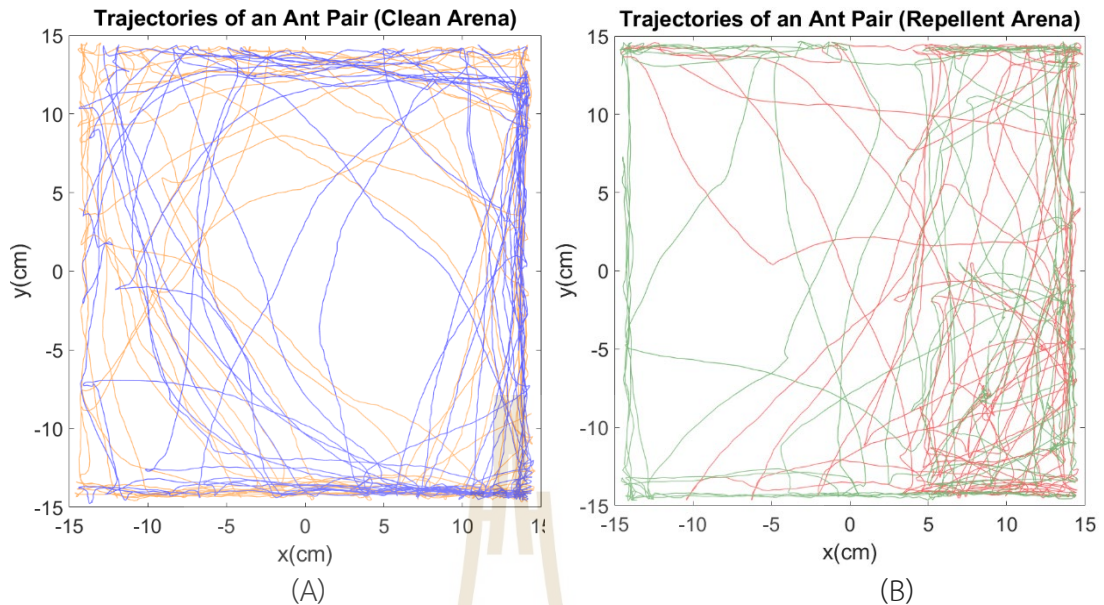
Throughout the 5-minute duration of a given trial, the ants remained in constant motion without any noticeable slowdown or behavioral change over time. A significant portion of their time was spent near the arena boundaries, repeatedly returning to the tile edge and appearing to pause at the bounding water. While they spent less time in the interior of the arena, they did frequently cross it while moving from one edge to another.

Ants showed a moderate aversion to the repellent in both SR and PR trials. Some ants would limit their movement to a clean area and avoid crossing the repellent. Others would exhibit reduced speed upon entering the repellent band, but still pass through it. On rare occasions, an ant would navigate the arena without any apparent concern or response to the presence of the repellent.

In PC and PR trials, the two ants primarily spent their time individually exploring the arena. However, they would frequently come near each other to pause for a brief interaction, and then continue their exploration separately. These meetings typically lasted between 1 and 3 seconds. There were no apparent variations in the frequency or length of these interactions over time. Although most of the meetings occurred within clean areas of the arena, we occasionally observed them taking place in the repellent area.



**Figure 4.1** (A) An example of trajectory of an ant in a clean arena (SC). (B) An example of trajectory of an ant in a repellent arena (SR).



**Figure 4.2** (A) An example of trajectories of an ant pair in a clean arena (PC). (B) An example of trajectories of an ant pair in a repellent arena (PR).

#### 4.1.2 Quantitative results

We fixed a relative small  $d = 1$  cm square size, which is roughly equal to the ant body length, when we compiled the correlation function  $G(d, \tau)$ . So, contributions to the correlation function require ants to be near enough to make contact (of course they could only do so if  $\tau = 0$ , i.e. they were both in this  $d$ -length square at the same time). With the value of  $d$  fixed, we have a simple function  $G(1, \tau)$  of one variable, the time  $\tau$ . The function should contain dynamic information about correlation/communication between ants. We can calculate the function  $G(\tau)$  for any pair of ants, including ants in *different* arenas. Since a pair of ants in different arenas cannot interact, their measured  $G(1, \tau)$  provides a natural control group. When we measure  $G(1, \tau)$  for two ants in the same arena, the difference between the results and that for the control group is due mainly to ant-ant interaction. We note that this procedure is useful because the statistical distribution of an ant over the arena is not homogenous – an ant tends to spend most of its time near the arena boundary as

noted above. Thus, the probability to find an ant in a given  $d$ -length square is not  $(d/L)^2$  as it would be for a homogenous distribution.

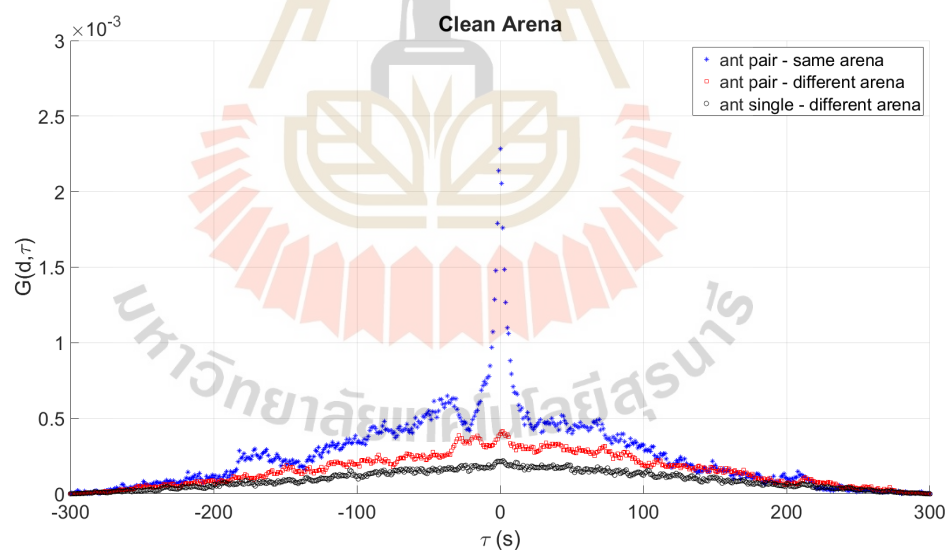
The average function  $G(\tau)$  over trials with paired ants is shown as the blue curve in Figure 4.3 (for PC) and 4.4 (for PR). We have a clear indication of dynamic correlation. The strong peaks at  $\tau = 0s$  means that ants are meeting. The distinctive shape of the peak contains additional information: within the shoulders of the peak an ant is arriving at a particular location a short time after its partner left it. The function  $G(\tau)$  for two uncorrelated ants are also shown in Figure 4.3 and 4.4 as red curves for ant pairs in *different* arenas and black curves for ant singles in *different* arenas (the control groups). The results showed that there were no strong peaks at  $\tau = 0s$  but the data was spread widely along the time scale for both cases. Showing weak  $\tau$  dependence.

Now consider what the correlation function has to say about ant hierarchy. Is one of the two paired ants leading the other? Recall that, in our original analysis, one ant was called A and the other B, but these labels had no significance—they were entirely arbitrary. Then, for each pair, we calculated  $G(\tau)$  and integrated it separately over positive and negative. If the  $\tau > 0$  integral was larger then B followed A more often than the other way around, so we assigned new labels with A=L as leader and B=F as follower. Conversely, if the  $\tau < 0$  integral was larger then we assigned B=L and A=F. Having relabeled the ants in this way, the average correlation function  $G(\tau)$  is certain to be asymmetric with more weight on the positive side because this is the side that corresponds to L leading and F following. That is, we constructed  $G(\tau)$  to make it as asymmetric as possible, with the  $\tau > 0$  integral certain to be larger than the  $\tau < 0$  integral. But if, despite this effort to tip the scales in favor of the putative leaders, we see no significant asymmetry in  $G(\tau)$ , then we can conclude strongly that there really are no leaders among ant pairs and the partnership is equitable.

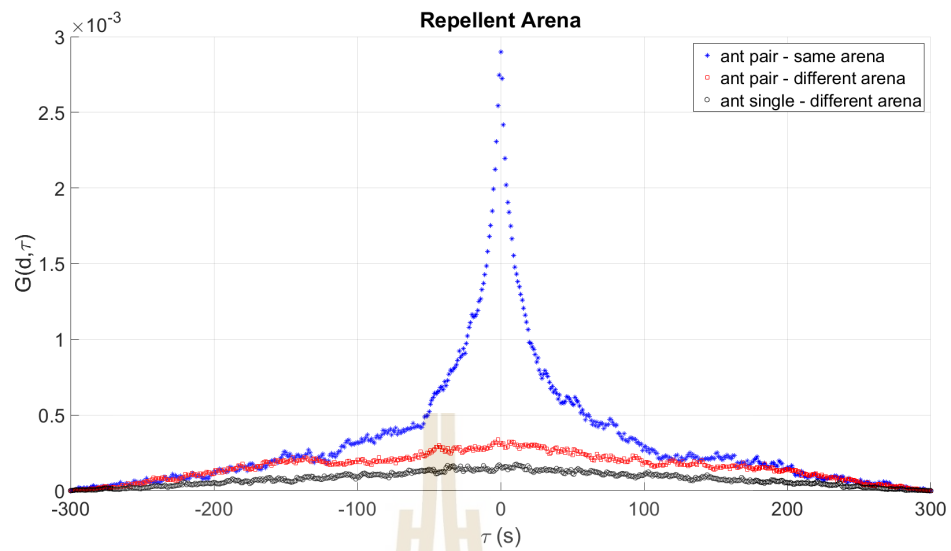
The results are shown in Figure 4.5 for clean arena and Figure 4.6 for repellent arena. The original AB pairing is shown as the blue curve. The only possible



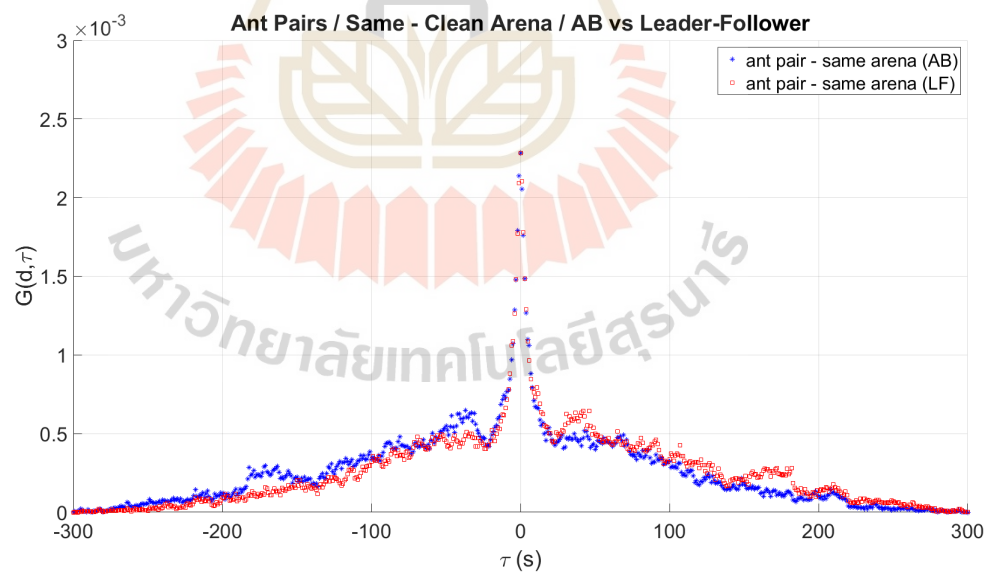
source of even-odd asymmetry in this curve is statistical noise, since the labels are arbitrary. Indeed, this curve appears symmetric to the eye. The relabeled LF pairing is shown as the red curve. Here one can see that the LF correlation function has more weight for  $\tau > 0$ , since the red curve lies above the blue curve, and less for  $\tau < 0$ , where the situation is reversed. Nonetheless, the LF curve appears symmetric to a very good approximation, and at first glance we would say  $G(\tau) = G(-\tau)$ . This indicates that if there is a tendency for one ant to act as leader and the other to accept a role as follower, then this tendency is weak. A slightly more detailed picture is provided by taking the difference between the  $G(\tau)$  curve with the LF labeling and that with the *original* AB labeling. This difference is plotted in Figure 4.7 for clean arena and Figure 4.8 for repellent arena. As before we note that the difference between the two curves is not dramatic, but that the LF curve has higher values for  $\tau > 0$  as it must.



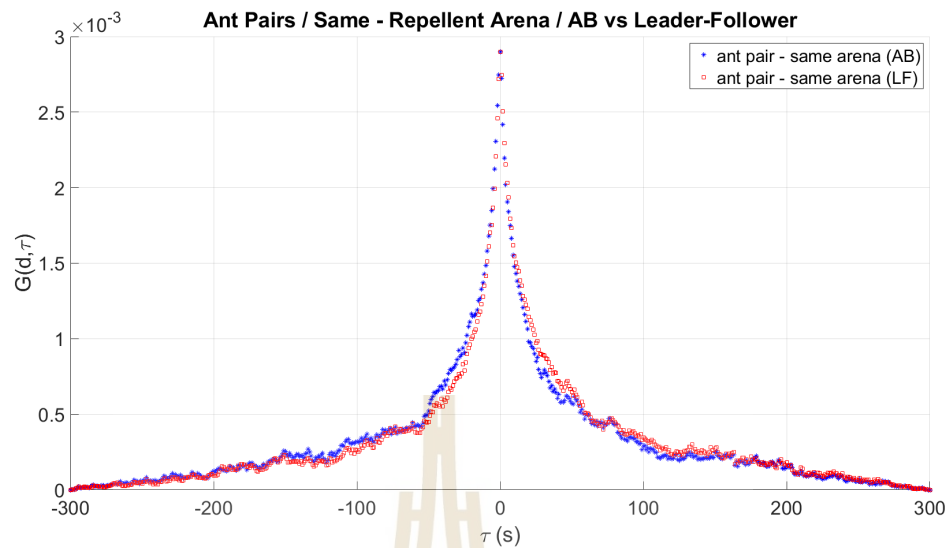
**Figure 4.3** Correlation function  $G(\tau)$  of the experimental group (PC) and the control groups (uncorrelated ants) in a clean arena.



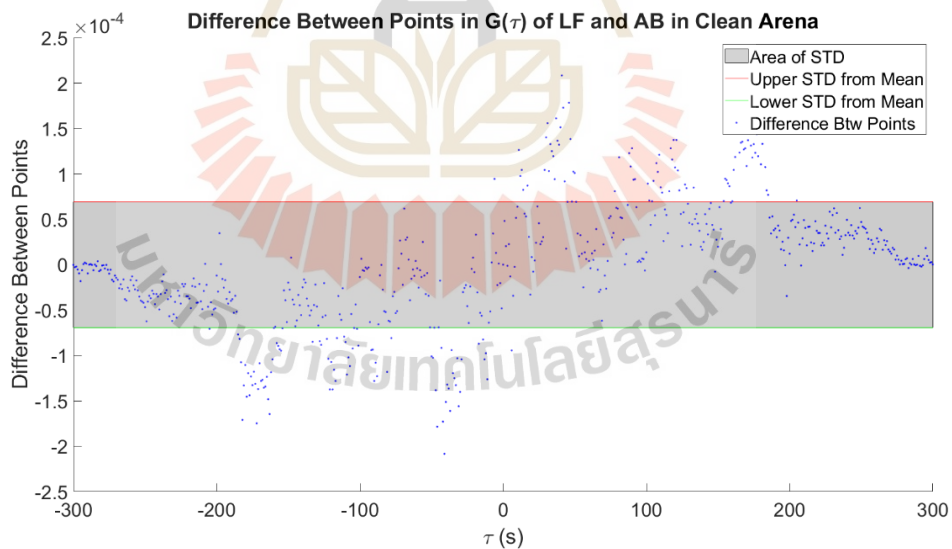
**Figure 4.4** Correlation function  $G(\tau)$  of the experimental group (PR) and the control groups (uncorrelated ants) in an arena partly coated with repellent.



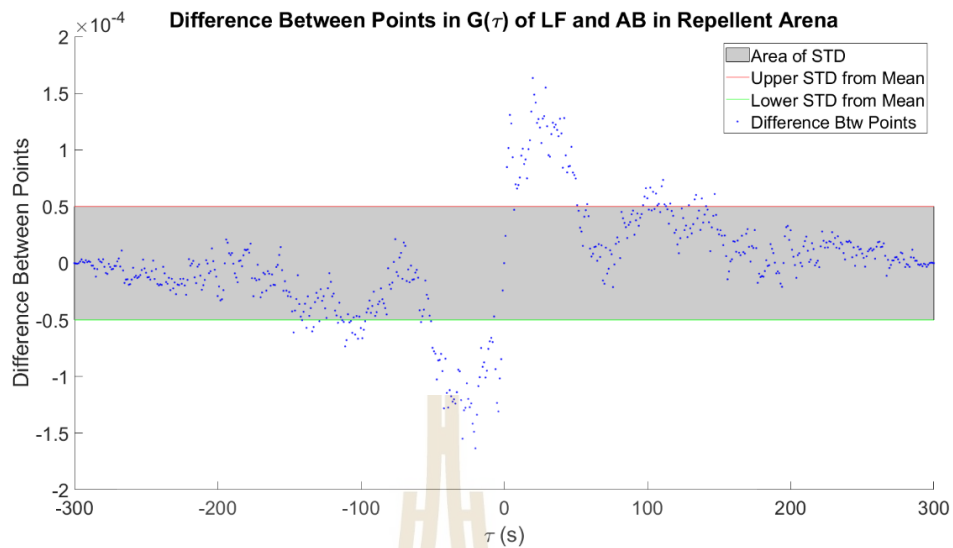
**Figure 4.5** Ant hierarchy in a clean arena. The *original* (A-B labeling) correlation function for the experimental group (PC) in blue versus the *leader-follower* (L-F labeling) correlation function for the experimental group (PC).



**Figure 4.6** Ant hierarchy in the arena partly coated with repellent. The *original* (A-B labeling) correlation function for the experimental group (PR) in blue versus the *leader-follower* (L-F labeling) correlation function for the experimental group (PR).



**Figure 4.7** The difference between points of the *original* (A-B labeling) correlation function for the experimental group (PC) versus the *leader-follower* (L-F labeling) correlation function for the experimental group (PC).



**Figure 4.8** The difference between points of the *original* (A-B labeling) correlation function for the experimental group (PR) versus the *leader-follower* (L-F labeling) correlation function for the experimental group (PR).

## 4.2 Discussions

The ants remained in constant motion without any noticeable slowdown or behavioral change over time. We previously tried durations of more than 5 minutes (15-minute duration, approximately) and still saw no obvious signs of fatigue in the ants. The 5-minute duration, while long enough to amass the required volume of statistical data, should be short enough that it does not introduce any time-dependent variables.

In the results for the calculation of the function  $G(\tau)$  in the experimental groups; PC and PR, as compared to the control groups (two ants in *different* arena) for both clean and repellent arenas, we see strong peaks at  $\tau = 0s$ . This in itself does not certainly indicate communication is taking place, though the frequency of the meetings and their time and position-dependence can be used to determine how the ants modify their navigation upon approaching and moving away from each other.

For the two correlations for the control groups shown in Figure 4.3 and 4.4, we noted that  $G(\tau)$  displayed weak  $\tau$  dependence. However, we can see that ant pairs in *different* arenas (in red) show a higher average  $G(\tau)$  value than do single ants in *different* arenas for both the clean and coated cases. This appears curious since there can be no real correlation in motion for either configuration. But consider the fact that paired ants often come together to meet, remaining in the same position for a second or two, and that these meetings most often take place in the regions where ants spend most of their time: near the boundary. Thus effect of meetings is likely to further increase the fraction of time that a given ant spends near the boundary. That is, a paired ant is more likely to be found at a given position within the narrow strip along the arena edge. Another paired ant, in a *different* arena, thus has a higher probability to occupy the equivalent position in its own arena. This would explain the enhancement of  $G(\tau)$  for the paired control group relative to the singles control group. This technical point is of little interest in itself, but does underscore the fact that it is the time dependence of  $G(\tau)$ , rather than its numerical value, that provides information about ant-ant correlation.

The results showed that the difference between  $G(d, \tau)$  and  $G(d, -\tau)$  is not *significant*, even for relabeled the pairs as L and F to make this plot as asymmetric as possible. So, we can claim that there is no real leader among the paired ants. Our results would suggest rather an equitable balance of power between the paired ants as far as navigating with in our arena is concerned.

However, there is an interesting comparison to be made between the results shown for the clean and coated (with repellent) arenas, in Figure 4.7 and 4.8. At first, glancing at those, which plots the difference  $D(d, \tau) = G_{LF}(\tau) - G_{AB}(\tau)$  between the correlation function calculated with leader-follower LF labels and that initially calculated with arbitrary AB labels, one notices that it exhibits exact odd symmetry,  $D(-\tau) = -D(\tau)$ . This is easily understood. The trials in which A=L (i.e. trials for which  $G_{AB}(\tau)$  had more weight for positive  $\tau$ ) contribute nothing to  $D(\tau)$  because the AB and

LF labels are equivalent. For trials where  $B=L$  (because  $G_{AB}(\tau)$  had more weight for negative  $\tau$ ) the AB and LF labels are swapped. Since swapping labels is the same as replacing  $\tau$  with  $-\tau$ , the function  $D(\tau)$  must be odd.

For the clean arena, the asymmetry seen for the LF data, as compared to the AB data, appears to be distributed roughly evenly over a wide range of  $\tau$ . For the coated arena, this asymmetry is dominated by small  $|\tau|$ . The reason this is significant is that the  $G(\tau)$  curves only contain information about ant-ant correlation at relatively small values of  $|\tau|$ . We saw this earlier, from the fact that the curves at large  $|\tau|$  were indistinguishable from the control groups, and thus reflective only of statistical noise. So, we can conclude that the asymmetry in the LF curves for clean arenas probably has no significance: it arises from statistical noise. On the other hand, the asymmetry in the LF curves for coated arenas may be meaningful since it arises at small  $|\tau|$  where correlations are occurring.

We should not overstate this finding, because the main takeaway from our result is that there is, at most, an extremely weak tendency for one ant to assume leadership over the other under any condition within the range of our experiments. But the fact that the only possible inequity in the ant pair relationship occurs in the presence of a chemical repellent is worth noting. If there is repellent in the arena then one ant could help the other avoid it by sharing information about previous experiences. It is plausible that the leader might be the member that first encountered, or is most tolerant to, the aversive chemical and thus has more information to share about the correct path needed to avoid it. This last point is speculative, but may motivate further inquiry into the possibility that leadership can emerge among ants under specific circumstances.



## CHAPTER V

### CONCLUSION

We studied the motion of weaver ants (members of *Oecophylla smaragdina*) under simplistic, artificial conditions. A square floor tile bounded by water was used as an arena within which ant motion was tracked. We let weaver ants, alone or as part of a pair, move freely around this arena for five minutes and measured their position with time. We studied the effect on motion of an aversive chemical, coated over one section of the arena, in some trials. But our main interest was the correlation between ant position, characterized by a time-dependent function  $G(\tau)$  that gives the probability that one ant of a pair, say the one arbitrarily labeled A, arrives at a given position within the arena and ant B arrives at the same position after a time delay of  $\tau$  seconds. This measurable quantity  $G(\tau)$  can be used to assess the strength of ant-ant correlations: the extent to which the motion of one ant affects that of the other; it can also give insight into a possible hierarchy among workers of a given weaver ant colony: as suggested by the relative probability that B follows A. Conveniently,  $G(\tau)$  can be measured for ants in different arenas, which obviously move independently, and ants in the same arena, which interact. The difference between results in these two cases isolates the effects of ant-ant correlation.

While networks of weaver ants are known to communicate in a sophisticated manner, our experiments revealed that, under certain conditions, their behavior can be simplistic and understandable. A given ant moved throughout the five-minute trial, showing no time-dependent behavior, and repeatedly visited the arena boundary without executing any regular search pattern. It usually reacted to the repellent, often slowing as it entered into a region coated with the repulsive chemical, but in some cases showed little sensitivity to the substance. Pairs of ants interacted frequently,

coming into close contact and interacting in some way, but their interactions exhibited no marked time or position dependence either.

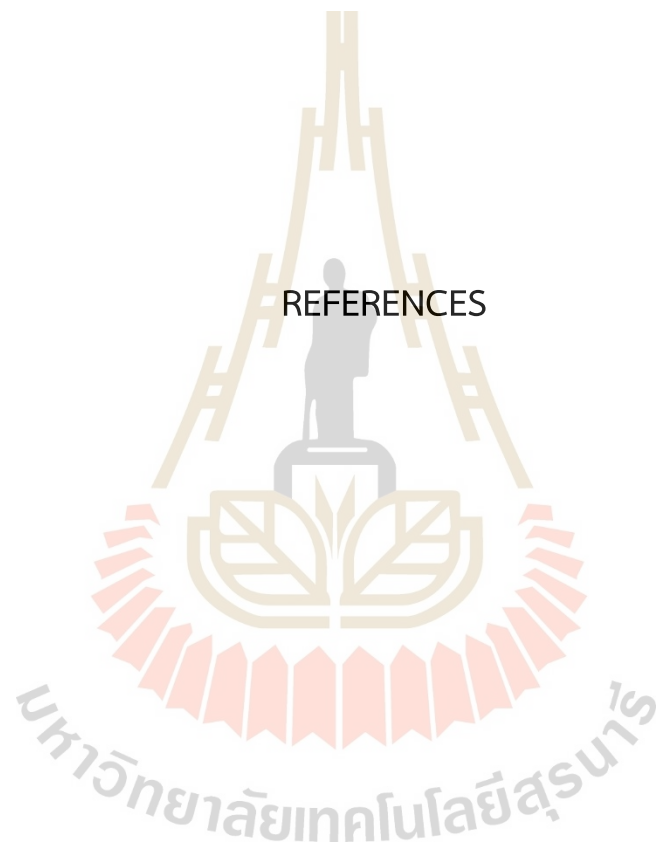
The correlation function  $G(\tau)$  revealed that ant pairs have highly correlated motion at small time differences, such that an ant is likely to arrive at a given location shortly after its partner. At large times, their motion is uncorrelated, being indistinguishable to that for ants in different arenas. Most interestingly, the function for a given ant pair approximately satisfied  $G(\tau) = G(-\tau)$ , which indicates an equitable partnership: A is just as likely to follow B as the other way around. Even when we biased the results, by assigning a putative leader L and follower F according to any small asymmetry for the pair then finding the average  $G(\tau)$  curve measured with this relabeling, we saw only a very weak tendency for one ant to exert more control over correlated motion than the other. The only possible exception was seen in the presence of a chemical repellent, where there was a more significant asymmetry observed between the assigned leaders and followers. This may suggest that, in the presence of the negative stimulus, one ant member is more likely to direct the motion of the other—perhaps as a result of one, having learned how to avoid the repellent, sharing helpful information to the other.

Our study makes a small contribution to the enormous literature on ant motion that has been amassed over centuries of study. We chose a species, readily available in Thailand, renowned for highly-organized collective behavior. We aimed to gain some insight into the effects on its observable motion of basic one-to-one communication. We found evidence that the isolated weaver ant individual, in an unfamiliar and featureless environment, moves stochastically. And while ant pairs do communicate, neither ant assumes a leadership role: the correlation of their motion exhibits symmetry. It is interesting to consider the possible implications for the nature of colony-wide correlated motion that enables the nest construction for which “weaver ants” are named. Are these large scale feats of cooperative action possible without

any hierarchy among members? We hope our preliminary work may be of some interest to those pursuing such deeper questions.



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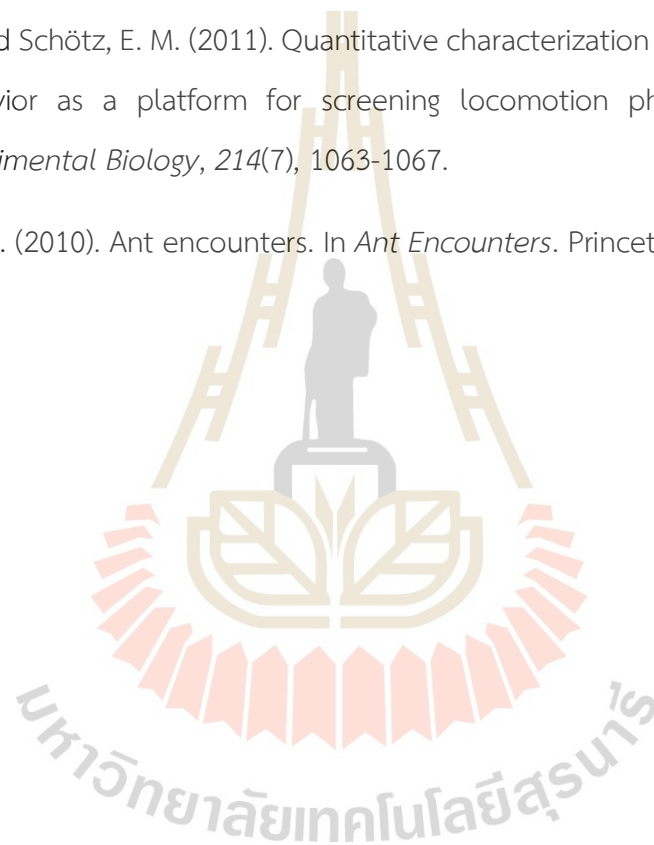


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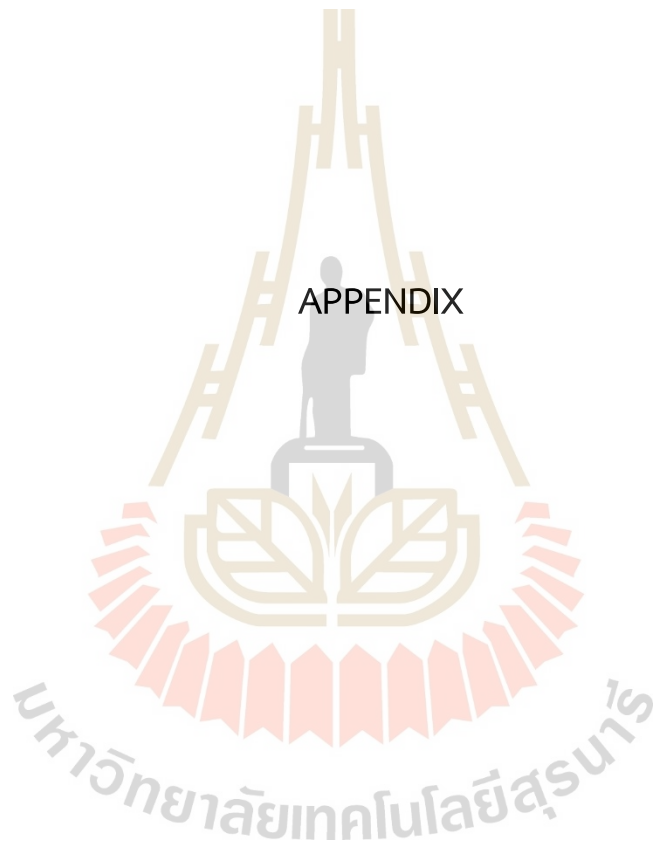
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APPENDIX

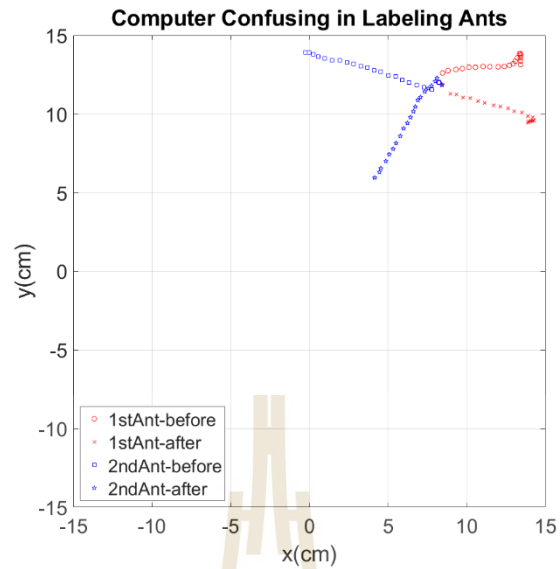


## APPENDIX

### COMPUTER CONFUSING

As we tried to track ants' motion in the arena by using our scripts coded in MATLAB R2018b program. There were some difficulties in tracking a pair of ants as we mentioned in CHAPTER III. That is, when a pair had come into close proximity at a particular time, the tracking algorithm was having a hard time in labeling ant A and B after they had separated. In Figure A.1, an example of many cases that happened after each of the image-based tracking was done. Ant A, in red circle, had come to the meeting point also ant B, in blue square, after the meeting the computer told us as in the figure, ant A went on the right side, in red cross, and ant B went downward, in blue star. This could be false if the ants continued walking with their momentums which sometimes they did, sometimes they did not.

Therefore, we had to verify if these were correct trajectories and fix it otherwise, by re-watching the relevant segment of the video footage. Of course, we did not watch the whole video again to see the corrections, instead we wrote some scripts to the program to tell us where and when the meeting was taking place then we matched with the video and made sure that every trajectory was correct.



**Figure A.1** Computer confusing in labeling ant A and B. Here is an example of many cases that occurred in the tracking process. Ant A's trajectory in red circle before the meeting point. Ant B' trajectory in blue square before the meeting point. Ant A's and B's trajectories after the meeting in red cross and in blue star, respectively.

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