

## RESEARCH ARTICLE

# Characteristics of daily foraging activity of *Camponotus japonicus* via time series analysis

Hiromichi Goko<sup>1\*</sup>, Osamu Yamanaka<sup>2</sup>, Masashi Shiraishi<sup>2</sup>, Hiraku Nishimori<sup>2</sup>

**1** Frontier Research Center, Toyota Motor Corporation, Toyota, Aichi, Japan, **2** Meiji Institute for Advanced Study of Mathematical Sciences, Meiji University, Nakano, Tokyo Japan

\* [tmcgoko@gmail.com](mailto:tmcgoko@gmail.com)

## Abstract

Social insects often share tasks among individuals. In this study, we analyzed the foraging activity of ants (*Camponotus japonicus*) and recorded the daily passage event counts of individual workers between a nest chamber and a foraging arena in five monodomous colonies. We proposed two hypotheses on the time series of foraging frequency by individual worker ants as follows: (i) for the time series of foraging frequency by individual worker ants, the foraging frequency on a certain day could be expressed by the product of the foraging frequency on the previous day and the exponential of a random number. (ii) The random numbers are correlated between some pairs of worker ants. The results for the five tested ant colonies showed that the probability of total daily passage counts (the sum of an individual's passage count) followed a log-normal distribution. The worker ants behaved differently in terms of active days and foraging frequency. However, for > 54% of the worker ants, the probability of the daily passage count was characterized by a log-normal distribution, and these worker ants performed > 72% of the tasks in each colony. Furthermore, for > 73% of the worker ants, the time development of the passage count was mathematically modeled; the logarithmic first difference between the passage counts on a certain day and those on the previous day was a random normal variable. These results support hypothesis (i). Additionally, the random numbers that were equivalent to the logarithmic first difference were correlated for some pairs of worker ants. These results support hypothesis (ii).

## OPEN ACCESS

**Citation:** Goko H, Yamanaka O, Shiraishi M, Nishimori H (2023) Characteristics of daily foraging activity of *Camponotus japonicus* via time series analysis. PLoS ONE 18(11): e0293455. <https://doi.org/10.1371/journal.pone.0293455>

**Editor:** Renier Mendoza, University of the Philippines Diliman, PHILIPPINES

**Received:** December 16, 2022

**Accepted:** October 12, 2023

**Published:** November 16, 2023

**Copyright:** © 2023 Goko et al. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

**Data Availability Statement:** The data will be held in a public repository. <https://doi.org/10.5061/dryad.c866t1gcp> The above URL will only be available after acceptance.

**Funding:** JST CREST grant numbers JPMJCR15D4 (MS and HN), JSPS KAKENHI grant number 16H04035(HN), 26610117(HN), 20H01871 (MS and HN). JSPS Transformative Research Areas Number 21H05297(HN, MS, and OY). MEXT Promotion of Distinctive Joint Research Center Program Grant Number JPMXP0620335886(HN). The funders had no role in study design, data

## Introduction

Worker ants share essential tasks to sustain their colony, such as caring for their broods, foraging for food, and protecting the colony from predators; the workload is too massive to be handled by an individual worker. The fact that the taxon has survived for 50 million years or longer implies that rational mechanisms of task allocation exist among workers, which aid in the sustenance of ant colonies [1]. The task allocation mechanisms of social insects have been explored theoretically [2] and experimentally [3, 4]. The colonies of social insects do not have leaders who supervise the workers [1]. Therefore, each worker chooses a task based on independent retrieval of external and internal information.

collection and analysis, decision to publish, or preparation of the manuscript.

**Competing interests:** The authors have declared that no competing interests exist.

To obtain external information, they walk inside and outside of their nest and contact other workers through trophallaxis and antennation. Humidity conditions outside the nest regulate the foraging activity of the workers. The workers do not walk outside when humidity is low because it can cause dehydration and death [5]. Workers allocated with a specific task often communicate with other similarly specialized workers [6].

As for the internal information, the circadian rhythm is crucial in controlling the activity of individual workers, especially when they engage in brood care [7] and foraging [8, 9]. Although the circadian rhythm is an intra-individual trait, it acts as an external cue for other individuals during social interactions. In the monomorphic ant *Diacamma*, the individual workers display circadian rhythm regardless of age [7]. The interaction amongst the young workers entrained their circadian rhythm, which amongst the old workers did not result in any change. The presence of young workers in a mixed group entrains the collective circadian activity rhythm of the group.

Genetic information is another type of internal information that determines individual behavior. For example, *Pheidole* workers present phenotypically defined bimodal body sizes [10]. The workers with larger heads mainly guard the nest, but they also nurse their brood in the event of a reduction in the number of nursing workers. As a result of the complex information-sharing processes within and among individual workers, they spontaneously engage in tasks, making them appear as though the ants are assigned specific functions in the colony.

Task allocation is a macroscopic phenomenon accompanied by fluctuations, thus, the statistical properties of the counts and times of tasks performed by workers have been studied to characterize task allocation [11–13]. For example, statistical analysis of workload distribution of an entire colony revealed that the proportion of diligent and lazy workers was maintained after removing a part of the worker populations [14] and the shape of the workload distribution curve varied depending on the type of task [11]. These distribution data were obtained from a time series of activity. However, the time series of foraging activity has not yet been fully characterized because it requires an enormous amount of data for statistical validation. In terms of time-variation of statistical properties, the activity of individual workers is dynamically transient over time, with the statistical property being constant overall [15].

The probability distributions can be expressed by heavy-tailed distributions such as Lévy flight and log-normal [16–19]. Previous studies have also revealed the origin of such distributions [20–22]. For example, log-normal distribution is obtained under a mathematical premise [23]. These studies deepened the comprehensive understanding of animal behaviors and their commonality.

The foraging activity is evidently a vital task exhibited by ants. In this study, we recorded the foraging activities of the ant species, *Camponotus japonicus*. The foraging activity of *C. japonicus* has not been sufficiently analyzed from a statistical viewpoint using massive amounts of time series data. Our study was based on the following hypotheses: (i) the foraging frequency on a certain day could be expressed by the product of the foraging frequency on the previous day and a random number. (ii) The random numbers are correlated between pairs of worker ants, indicating that they collaborate. The first hypothesis (hypothesis (i)) is regarding the daily foraging frequency by individual worker ants. The random number corresponded to external and internal information of an ant and a colony. The second hypothesis (hypothesis (ii)) suggests that ants collaborate.

The two hypothesis ((i) and (ii)) are related in the following context: First, hypothesis (i) implies that the time series of the daily foraging frequency (DFF) of individual worker ants complies with the multiplicative stochastic process [24], which generates a log-normal distribution of the corresponding variable. To check whether this mathematical discussion was met in our study, we examined the log-normality of the distribution of DFF. Next, we explored the

daily sum distribution of the foraging frequency of all ants in each colony and confirmed its log-normality. Notably, it has mathematically been recognized that the sum of different groups of random variables, each of which obeys a log-normal distribution, does not generally exhibit a log-normal distribution if the random variables in different groups are uncorrelated [25].

A logical suggestion obtained from the above two discussions, in conjunction with discussions from mathematical and experimental viewpoints, suggests a correlation of foraging behavior between different ants in each colony. To validate this suggestion, we analyzed the time-series correlation of daily foraging activities of different ants and confirmed its reliability.

## Materials and methods

### Materials and animal care [15]

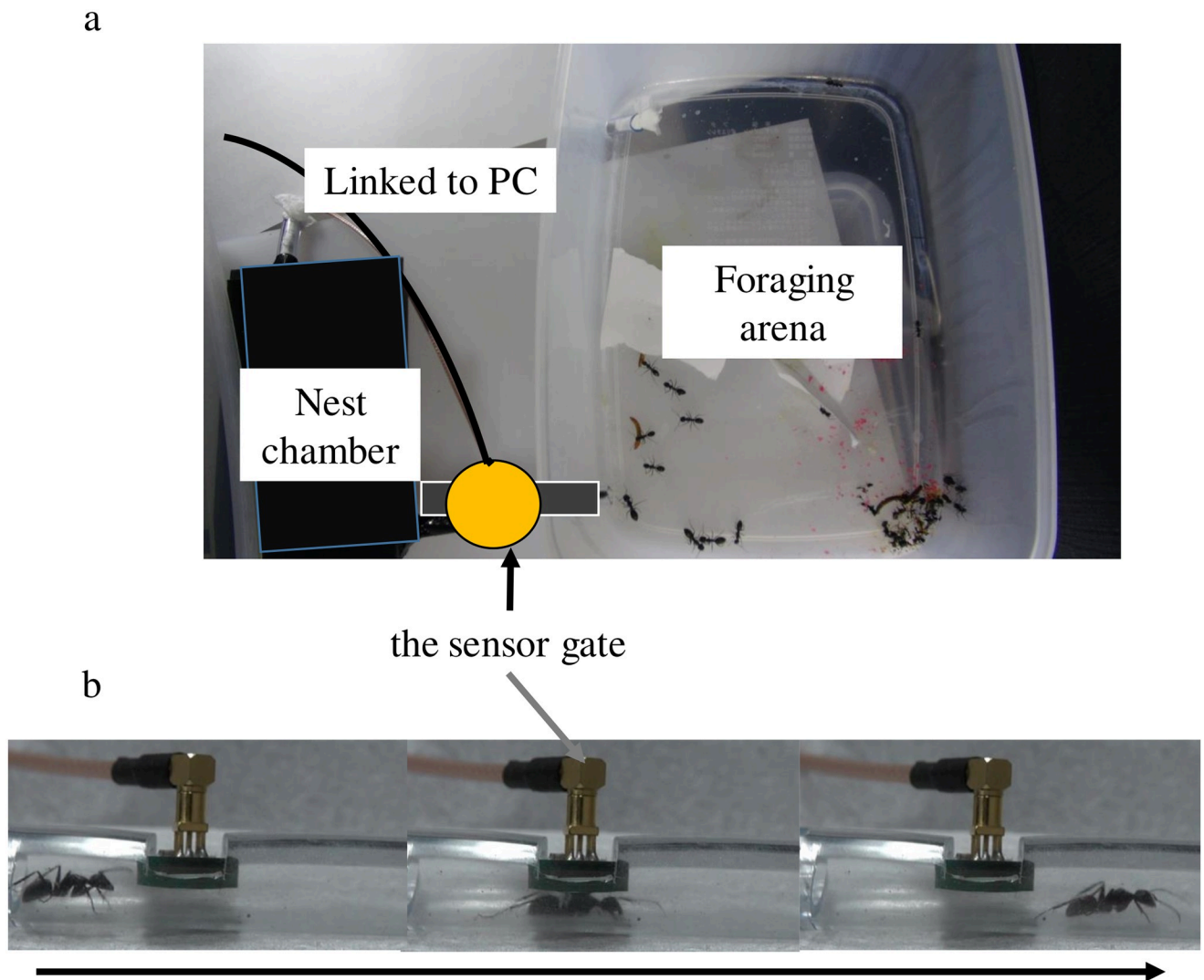
Five colonies of *Camponotus japonicus* were collected from the Higashi-Hiroshima campus, Hiroshima University between June 2015, and June 2018. *Camponotus japonicus* is monogynous and polymorphic (the body size of an individual worker ranges from 7– to 12mm). The ant colonies A, B, and C, contained one queen each, whereas the two remaining colonies, D and E, were without a queen. Each colony had approximately 150 workers. The colonies were maintained in plastic cases patched with plaster to maintain humidity and wrapped in tape to prevent exposure to light.

### Experimental setup

All five monodomous colonies were maintained in an experimental setup consisting of a nest chamber and a foraging arena as shown in Fig 1a. The nest chamber and the foraging arena were connected by a rubber tube. The walls in the foraging arena were coated with Fluon to prevent workers from escaping. The experiment was performed in a room where a 12h light-dark daily cycle was maintained starting at 8 : 00 when the LED lights were switched on; the temperature was 25°C, and the humidity was higher than 50%. We added insect jelly continuously and mealworms once every 2 days in the foraging arena to maintain the foraging activity of the workers. Experiments were conducted from May 1, 2015, to August 18, 2015 (Colony A); from June 3, 2018, to October 1, 2018 (Colony B); from June 6, 2018, to October 1, 2018 (Colony C); and from June 26, 2018, to October 1, 2018 (Colonies D and E). All colonies were recorded on all days during their respective experimental periods using a radio frequency identifier (RFID) measuring system.

### RFID tag attachment to individual workers [15]

Radio frequency identification (RFIDs) (SK-Electronics CO., Ltd., Japan) with unique identification numbers were attached to the thoraxes of each worker ant but not the queen ants, using an acrylic resin glue (Kiyohara UVR) (KIYOHARA & Co., Ltd.) without exposure to CO<sub>2</sub>. The RFID tag weights were lower than those used in other studies [26–29]; therefore, the effect of the tags on worker behavior was considered negligible. After the RFID tags were attached to 10 workers, they were placed in a case and irradiated with ultraviolet light for 30 min to harden the glue. This process was repeated for all workers. Thereafter, they were released into the foraging arena before they returned to the nest chamber. Workers equipped with tags took almost one week to acclimatize to the new nest chamber and foraging arena. Considering the adjustment period, experiments were started 1 week after the workers entered the nest chamber. Newly emerged workers were not equipped with RFID tags. An RFID reader (hereafter referred to as the “sensor gate”) was attached to the inner, upper surface of the center of the rubber tube that connected the foraging arena and the nest chamber (Fig 1). The RFIDs of



**Fig 1. Experimental setups.** Automatic system for measuring the foraging activity of *Camponotus japonicus* colonies using tiny radio frequency identification (RFID) tags. (a) Top view of the experimental setup. (b) Side view of the sensor gate and snapshots of a passage event of an ant moving from the nest chamber (left) to the foraging arena (right) in a time sequence.

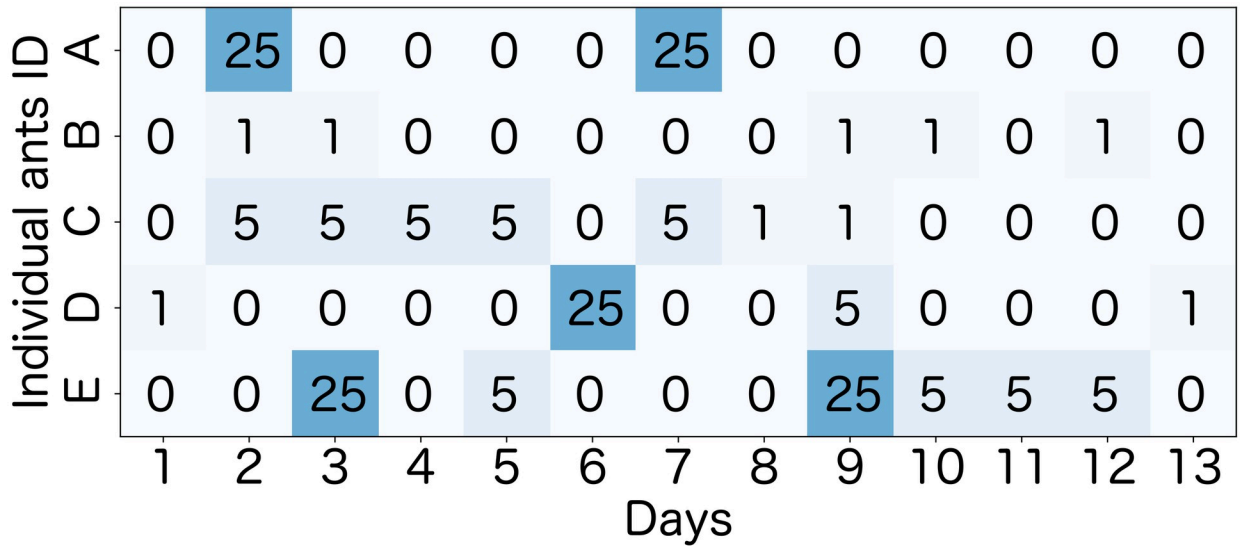
<https://doi.org/10.1371/journal.pone.0293455.g001>

individual workers and corresponding time stamps were automatically recorded. The passage direction to and from the nest chamber and the foraging arena was not distinguishable by this system.

### Data selection

We collected data from worker ants whose main task was foraging. We excluded all other workers that foraged only a few times or once over a prolonged period because they were engaged in other main tasks besides foraging. The selected worker ants satisfied three conditions:

- (I). The total number of passage events during its active period was at least 30.
- (II). The active period was at least 10 days.



**Fig 2. Virtual data of the foraging frequency of five ants in 13 days.** Each number in the grid represents the foraging frequency of individual ants on a particular day. The shade of the background color indicates the intensity of foraging frequency. The active period, the active days, the number of passage events, and the satisfied condition for each virtual ant are shown in Table 1.

<https://doi.org/10.1371/journal.pone.0293455.g002>

(III). An ant was active on at least half of the days during its active period.

The “active period” was defined as the set of days, from the first day to the last day, during which an ant made at least one passage event.

If a passage event was recorded on a certain day, we termed this day an “active day” and the ant an “active worker ant” of the day. For the time series analysis, we added 1 to the number of passage events in each day during the active period to avoid calculating log0.

Fig 2 illustrates virtual data that consists of the foraging frequency of five ants in 13 days. In this case, only *Ant E* was selected as a worker ant because it met the above three conditions, (I), (II), and (III)(see Table 1).

### Statistical analyses

**Static analysis.** In the case of individual worker ants, hypotheses (i) could be expressed as follows.

$$n_{i,t} = n_{i,t-1} \exp(\epsilon_{i,t}). \tag{1}$$

where  $n_{i,t}$  was defined as the count of passage events of the ant  $i$  on the day  $t$  and  $\epsilon_{i,t}$  was an independent normal random variable. Note that  $n_{i,t}$  were hypothesized to be correlated for some pairs of ants (hypothesis (ii)).

**Table 1. Active period, active days, the number of passage events, and satisfied condition for the five virtual ants in Fig 2.**

Individual Ant ID	Active period	Active days	The number of passage events	Satisfied conditions
A	6	2	50	(I)
B	11	5	6	(II)
C	8	7	27	(III)
D	13	4	32	(I),(II)
E	10	6	70	(I),(II),(III)

<https://doi.org/10.1371/journal.pone.0293455.t001>



Using simple mathematical discussion, we can recognize that, if Eq (1) holds and  $\epsilon_{i,t}$  is an independent normal random variable, static distribution of passage event count (SDPEC) forms a log-normal distribution [30]. In other words, the log-normality of the distribution of SDPEC is the necessary condition that Eq (1) holds. A normal distribution appears under a wide range of situations; if an independent random variable has a finite variance, its sum tends to follow a normal distribution.

The probability distribution of the total count of passage events was examined. We performed a Kolmogorov-Smirnov (KS) test on the null hypothesis that  $N_t$  was log-normally distributed. Whether  $N_t$  defined as  $\sum_{i \in W_t} n_{i,t}$  was log-normally distributed, as mentioned in the Introduction, and was related to hypothesis (ii). Next, the SDPEC of each ant from each colony was examined. For each ant  $i$ , the KS test was performed to assess the null hypothesis that  $n_{i,t}$  was log-normally distributed (hypothesis (i)).

**Time series analysis.** We examined the stationarities of  $n_{i,t}$  and  $\log n_{i,t}$ , as well as their first differences. If stationary, they indicated stochastic processes whose parameters (such as means and variances) changed when shifted in time. Hence, it is appropriate to model the whole investigated period as a simple stochastic process [31]. To evaluate the null hypothesis that  $n_{i,t}$  and  $\log n_{i,t}$  were non-stationary, an augmented Dickey-Fuller (ADF) test was conducted.

Then, the stationarity of the first differences of  $n_{i,t}$  and  $\log n_{i,t}$  were evaluated, respectively. The first differences,  $n_{i,t} - n_{i,t-1}$  and  $\log n_{i,t} - \log n_{i,t-1}$ , were defined as  $\epsilon_{i,t}^e$  and  $\epsilon_{i,t}$ , respectively. The ADF test was used to assess if  $\epsilon_{i,t}^e$  and  $\epsilon_{i,t}$  were non-stationary. Then, the distribution of  $\epsilon_{i,t}$  was examined. To assess the null hypothesis that  $\epsilon_{i,t}$  follows a normal distribution (hypothesis (i)), the KS test was performed on  $\epsilon_{i,t}$ .

Whether  $\epsilon_{i,t}$  depended on other worker ants in the same colony was also examined (hypothesis (ii)). The Pearson correlation coefficient  $\rho_{i,j}$  between  $\epsilon_{i,t}$  and  $\epsilon_{j,t}$  was calculated as follows:

$$\rho_{i,j} = \sum_{t \in W_{ij}} \text{correl}(\epsilon_{i,t}, \epsilon_{j,t}), \tag{2}$$

where

$$\text{correl}(\epsilon_{i,t}, \epsilon_{j,t}) = \frac{(\epsilon_{i,t} - \bar{\epsilon}_i)(\epsilon_{j,t} - \bar{\epsilon}_j)}{\sqrt{\sum_{t \in W_{ij}} (\epsilon_{i,t} - \bar{\epsilon}_i)^2} \sqrt{\sum_{t \in W_{ij}} (\epsilon_{j,t} - \bar{\epsilon}_j)^2}}. \tag{3}$$

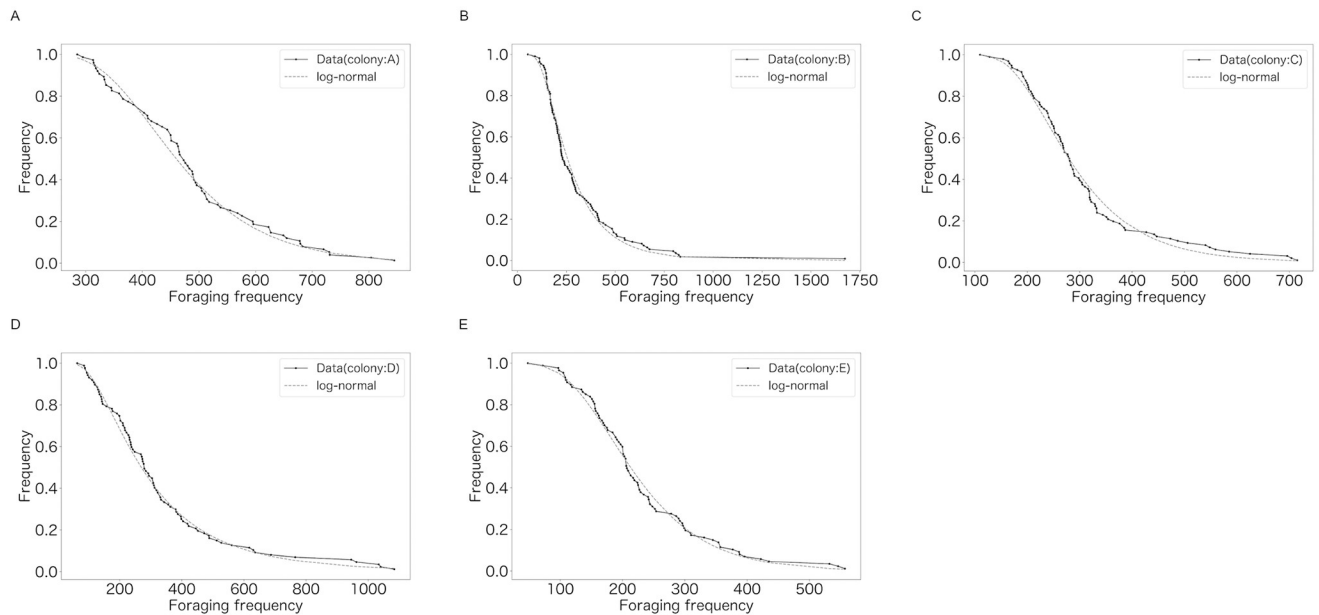
$W_{i,j}$  is the set of days in which worker ants  $i$  and  $j$  are both active.  $\bar{\epsilon}_k (k \in \{i, j\})$  was defined as follows.

$$\bar{\epsilon}_k = \frac{\sum_{t \in W_{ij}} \epsilon_{k,t}}{\sum_{t \in W_{ij}} 1}. \tag{4}$$

We calculated  $\rho_{i,j}$  only for the pairs of days  $(i, j)$  satisfying  $T_{i,j} \geq 10$ , where  $T_{i,j}$  is the overlap period between the active period of the ant  $i$  and that of ant  $j$  (see Subsection *Data selection* and Fig 2 for the definition of active period).

If Eq (1) holds and  $\epsilon_{i,t}$  is an independent normal random variable, then  $N_t$  does not generally distribute log-normally. Then, there may exist a correlation between  $\epsilon_{i,t}$ 's. Mathematically, hypothesis (ii) was related to this suggestion.

**Confidence level.** Our statistical significance level was set at ( $p$  value)  $< 0.05$  for both static and time series analyses.



**Fig 3. Cumulative probability distributions of  $N_t$ .** The solid lines represent the data. The dashed lines represent the lines of best fit. (A) Colony: A. (B) Colony: B. (C) Colony: C. (D) Colony: D. (E) Colony: E.

<https://doi.org/10.1371/journal.pone.0293455.g003>

## Results

Observation error, selection effect and summary statistics are shown in supporting information. Here, to clearly demonstrate the obtained results, before describing the details, we show our logical flow to examine the hypotheses by identifying the role of each table and figure.

Fig 1 shows the experimental setups. Fig 2, S1 Fig and Table 1 show images and characteristics of data. S1–S7 Tables show characteristics of the data such as summary statistics. Table 3 and Fig 4 show that the distribution of foraging frequency is consistent with the hypothesis (i). Tables 4 and 5 are the main results that support the hypothesis (i). Next, “random number” in the hypothesis is identified (Table 6). Additionally, Table 2 and Fig 3, together with hypothesis (i), suggest that hypothesis (ii) holds. However, as described in the last part of the introduction, this suggestion based on a mathematical discussion is still not complete. Thus, to complete the logic, we show Figs 5–7 and Table 7 which directly indicate the validity of the hypothesis (ii).

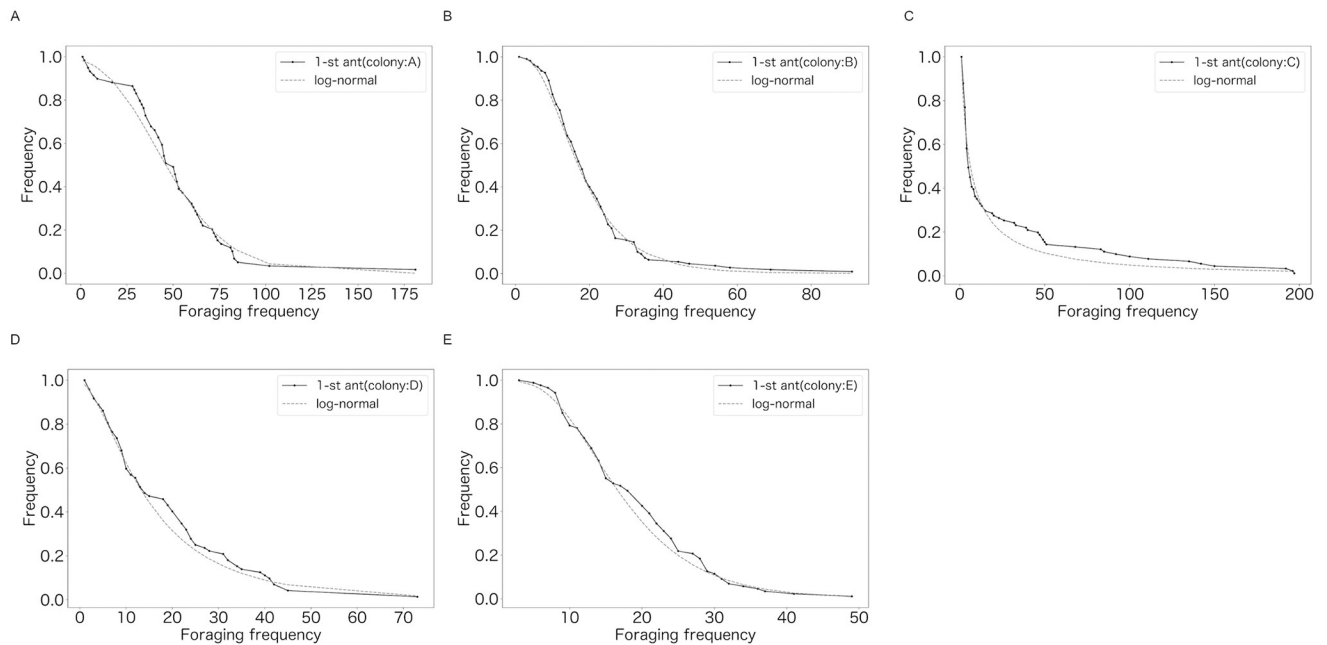
## Static analysis

The null hypothesis that  $N_t$  was log-normally distributed was not rejected for any colony (Table 2 and Fig 3).

**Table 2. Results of the Kolmogorov-Smirnov (KS) test for log  $N_t$ .**

Colony	p value
A	0.638086
B	0.348316
C	0.416029
D	0.906069
E	0.871890

<https://doi.org/10.1371/journal.pone.0293455.t002>



**Fig 4. Cumulative probability distributions of  $n_t$  for the most active ant in 5 colonies.** The solid lines represent the data. The dashed lines represent the lines of best fit. (A) colony: A. (B) colony: B. (C) colony: C. (D) colony: D. (E) colony: E.

<https://doi.org/10.1371/journal.pone.0293455.g004>

The results of the KS test, to test the null hypothesis that  $n_{i,t}$  was log-normally distributed for five colonies, are shown in Table 3. The results for the most active worker ants, showing the largest number of passage events in each colony, are shown in Fig 4. The null hypothesis was not rejected for at least 54.8% of the active worker ants. The proportion of passage events of worker ants that were assumed to have a log-normal distribution was at least 72.4%.

### Time series analysis

The null hypothesis that  $n_{i,t}$  was non-stationary was not rejected for more than half of the samples in three colonies (A, C, and E) (Table 4). For stationarity of  $\log n_{i,t}$ , the null hypothesis was not rejected for more than half of the samples in any colony (Table 4). The null hypothesis that  $\epsilon_{i,t}^e$  and  $\epsilon_{i,t}$  were non-stationary was rejected for more than 83.8% and 81.1% of the samples, respectively (Table 5). The null hypothesis that  $\epsilon_{i,t}$  follows a normal distribution was not rejected for at least 73.7% of the samples in each colony (Table 6). For those samples where  $\epsilon_{i,t}$

**Table 3. Results of the Kolmogorov-Smirnov (KS) test for  $\log n_{i,t}$ .** The second column shows the sample size for each colony. The third column shows the percentage of samples with  $p$  values  $\leq 0.05$  to the numbers of active worker ants. The fourth column shows the passage counts by samples with  $p > 0.05$ . The 5th column shows the percentage of passage counts by samples with  $p > 0.05$  to passage counts by active worker ants.

Colony	Samples ( $p > 0.05$ )	Samples (%) ( $p > 0.05$ )	Passage counts ( $p > 0.05$ )	Passage counts (%) ( $p > 0.05$ )
A	23	54.8	26626	73.7
B	38	71.7	27448	81.6
C	38	66.7	21191	72.4
D	47	67.2	24703	85.6
E	31	83.8	18287	91.5

<https://doi.org/10.1371/journal.pone.0293455.t003>



**Table 4. Results of the augmented Dickey-Fuller (ADF) test for  $n_{i,t}$  and  $\log n_{i,t}$ .** The second column shows the sample size of each colony. The third and fourth columns show the numbers of samples for which  $n_{i,t}$  was stationary at the 5% confidence level and their percentages, respectively. The fifth and sixth columns show the numbers of samples for which  $\log n_{i,t}$  was stationary at the 5% confidence level and their percentages, respectively.

Colony	Number of samples	$n_{i,t}$	Col3/Col2 (%)	$\log n_{i,t}$	Col5/Col2 (%)
A	42	18	42.9	11	26.2
B	53	34	64.2	25	47.2
C	57	14	24.6	8	14.0
D	61	41	67.2	16	26.2
E	37	18	48.6	13	35.1

<https://doi.org/10.1371/journal.pone.0293455.t004>

**Table 5. Results of the augmented Dickey-Fuller (ADF) test for  $\epsilon_{i,t}^e$  and  $\epsilon_{i,t}$ .** The second column shows the sample size of each colony. The third and fourth columns show the numbers of samples for which  $\epsilon_{i,t}^e$  was stationary at the 5% confidence level and their percentages, respectively. The fifth and sixth columns show the numbers of samples for which  $\epsilon_{i,t}$  was stationary at the 5% confidence level and their percentages, respectively.

Colony	Number of samples	$\epsilon_{i,t}^e$	Col3/Col2 (%)	$\epsilon_{i,t}$	Col5/Col2 (%)
A	42	39	92.9	41	97.6
B	53	46	86.8	47	88.7
C	57	51	89.5	50	87.7
D	61	55	90.2	55	90.2
E	37	31	83.8	30	81.1

<https://doi.org/10.1371/journal.pone.0293455.t005>

can be assumed to have a normal distribution,  $n_{i,t}$  can be written as follows:

$$n_{i,t} = n_{i,t-1} \exp(\epsilon_{i,t}^*), \tag{5}$$

where  $\epsilon_{i,t}^*$  follows normal distribution.

The absolute values of  $\rho_{i,j}$  were larger than 0.2 for at least 43.9% of the samples in each colony (Fig 5 and Table 7). Correlations were significant ( $p < 0.05$ ) for at least 19.0% of the sample in each colony (Fig 6 and Table 7). We observed  $T_{i,j} < 10$  in 21.0%(colony A), 4.2%(colony B), 23.9%(colony C), 11.6%(colony D), and 16.9%(colony E) of the samples. The frequency distribution of  $\rho_{i,j}$  was skewed to the left, and the value of  $\rho_{i,j}$  was more likely to be positive, except for colony A (Fig 7).

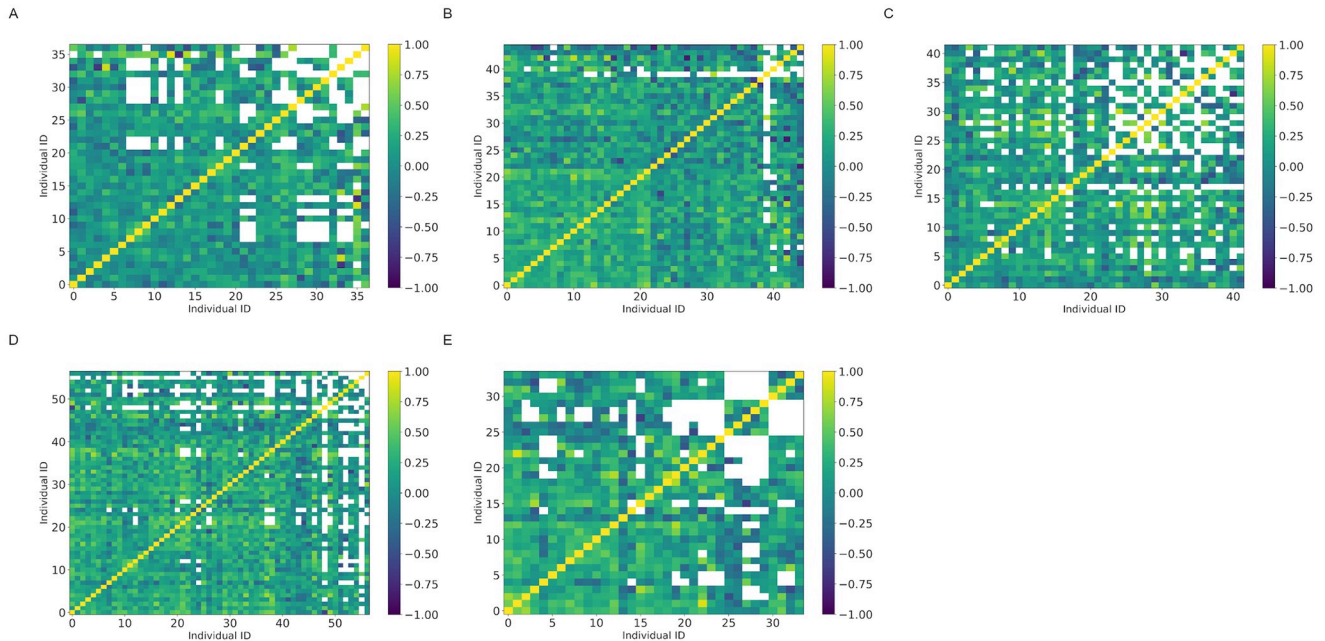
## Discussion

For most of the worker ants in this study, SDPEC could be characterized by a log-normal distribution, and the time development of  $n_{j,t}$  could be denoted by Eq (5). SDPEC of all the

**Table 6. Results of the Kolmogorov-Smirnov(KS) test for normality on  $\epsilon_{i,t}^{log}$ .** Numbers of samples with p values  $\geq 0.05$  are shown in the third column. The 5th and 6th columns show total passage counts of worker ants in column 2 and column 3, respectively.

Colony	Number of samples	Samples with $p \geq 0.05$	Col3/Col2 (%)	Passage counts (col2)	Passage counts (col3)	Col6/Col5 (%)
A	42	37	88.1	36148	34543	95.5
B	53	45	84.9	33623	30156	89.6
C	57	42	73.7	29265	21674	74.0
D	61	57	93.4	28873	28532	98.8
E	37	34	91.9	19982	19065	95.4

<https://doi.org/10.1371/journal.pone.0293455.t006>



**Fig 5. The Pearson correlation coefficient  $\rho_{ij}$  between  $\epsilon_{i,t}$  and  $\epsilon_{j,t}$ .** Vertical and horizontal axes correspond to each worker ant. Colors are differentiated according to the value of  $\rho_{ij}$ . White represents  $T_{ij} \leq 10$ . (A) Colony: A. (B) Colony: B. (C) Colony: C. (D) Colony: D. (E) Colony: E.

<https://doi.org/10.1371/journal.pone.0293455.g005>

selected worker ants in each colony could be characterized by a log-normal distribution. The results are consistent with hypothesis (i).

The fact that the first differences of  $n_{i,t}$  were stationary showed that Eq (5) is valid throughout the active periods. In other words, the daily foraging frequency of the worker ants could be expressed by a single mathematical model throughout their active periods. This suggests the universality of our mathematical model (Eq (5)); the law that expresses the foraging frequency of worker ants does not change regardless of their identity, age, and experience.

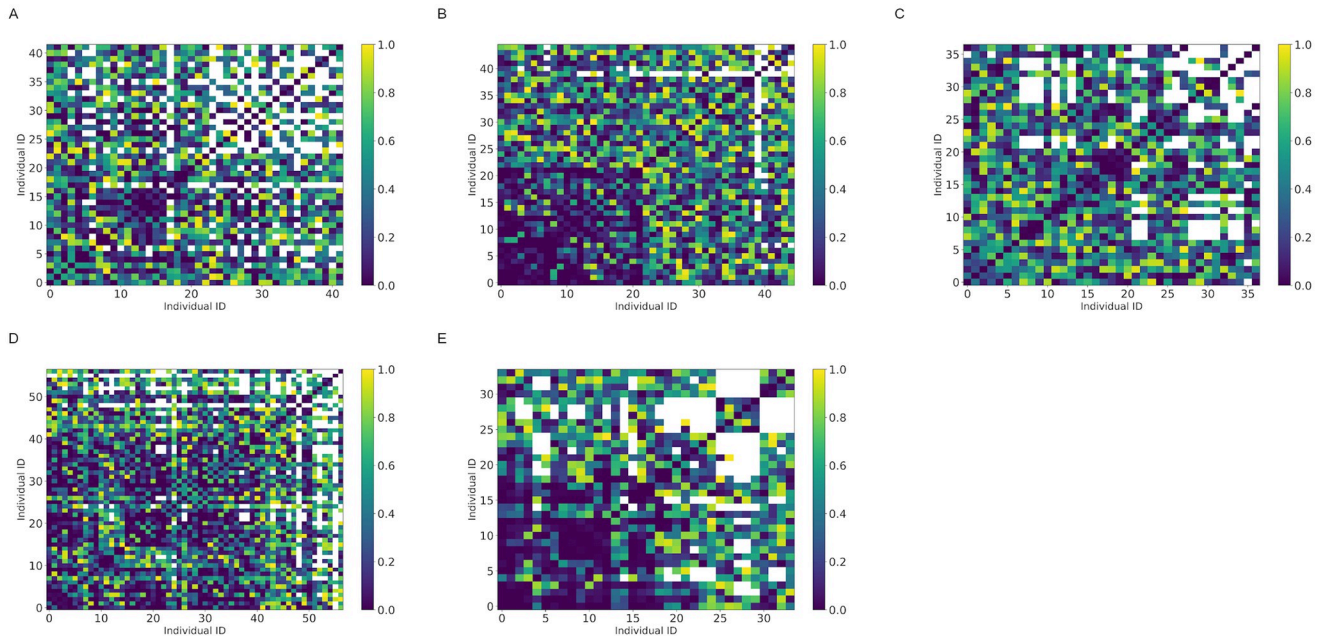
As mentioned in section *Introduction* and subsection *time series analysis*, if multiple variables are randomly and independently generated from a log-normal distribution, their sum does not generally follow a log-normal distribution. As both  $n_{i,t}$  and  $N_t$  followed a log-normal distribution, it indicates that  $n_{i,t}$  was not independent of  $n_{j,t}$  ( $i \neq j$ ). We found that  $\rho_{i,j}$  was substantially different from 0 in some cases. This fact supports hypothesis (ii). The correlation of foraging activities of the worker ants should play a vital role in generating a log-normal distribution of  $N_t$ . The correlation coefficients  $\rho_{i,j}$  were likely to be positive.

The source of the correlation remains unknown. One possible explanation for this is that if a colony needs to increase its food reserves, some worker ants communicate with each other,

**Table 7. Percentage of samples that satisfy  $|\rho_{i,j}| > 0.2$ (second column),  $p < 0.05$ (third column), and both conditions(fourth column).**

Colony	$ \rho_{i,j}  > 0.2$	$p < 0.05$	$ \rho_{i,j}  > 0.2 \ \& \ p < 0.05$
A	43.9	19.0	19.0
B	64.7	39.3	39.2
C	53.1	23.8	23.8
D	66.3	43.6	43.6
E	48.5	21.5	21.5

<https://doi.org/10.1371/journal.pone.0293455.t007>

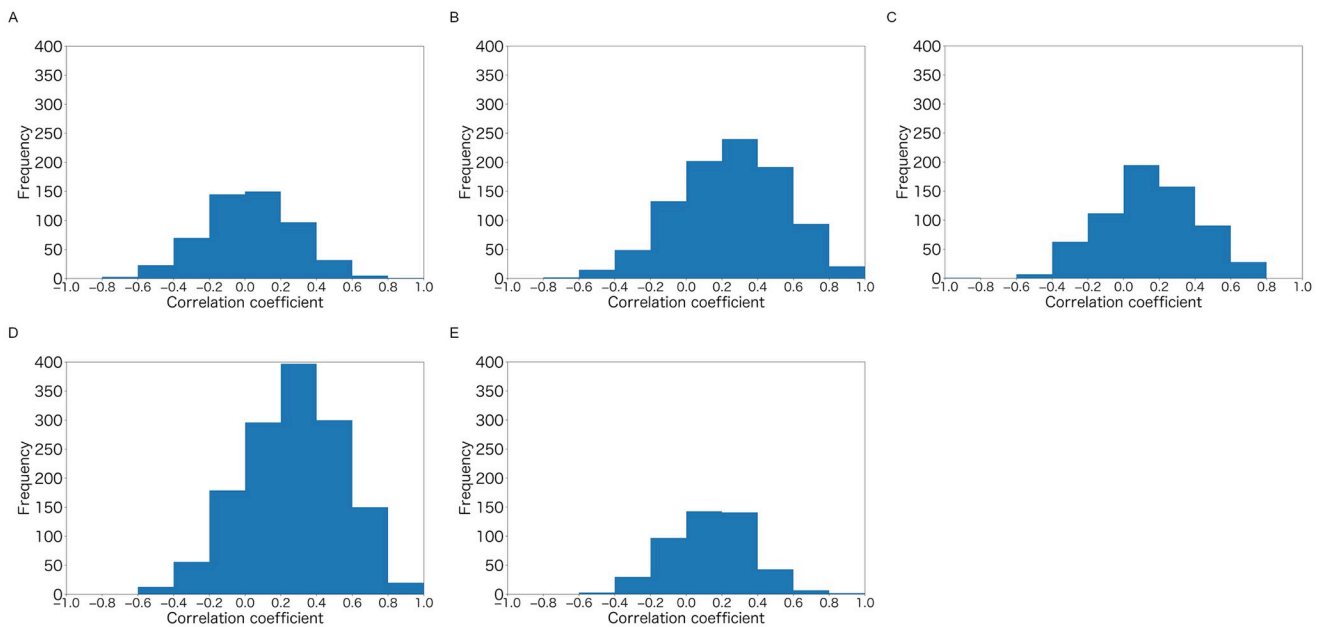


**Fig 6. P value for the Pearson correlation coefficient.** Vertical and horizontal axes correspond to each worker ant. Colors are differentiated according to the  $p$  value. White represents  $T_{ij} \leq 10$ . (A) Colony: A. (B) Colony: B. (C) Colony: C. (D) Colony: D. (E) Colony: E.

<https://doi.org/10.1371/journal.pone.0293455.g006>

in the time scale of day or longer, to recognize as a group that they should increase the foraging frequency.

On the shorter timescale, the interaction among workers is essential to generate the periodicity of activity levels of groups of workers [32, 33]. Moreover, the individual movement in the



**Fig 7. Frequency distribution of the Pearson correlation coefficient  $\rho_{ij}$  between  $\epsilon_{ij}$  and  $\epsilon_{ji}$ .** (A) Colony: A. (B) Colony: B. (C) Colony: C. (D) Colony: D. (E) Colony: E.

<https://doi.org/10.1371/journal.pone.0293455.g007>

timescale of seconds has universal relation between the velocity and the duration of moving, and the universality is not affected by the social interactions [34].

The relationship between social interactions and the correlation of activity in multiple time-scales could generate a long-term correlation. However, certain kinds of social interactions change the temporal characteristics of individual workers [7]. Therefore, it is important to specify what kind of social interaction affects the different timescale correlations in future work.

## Conclusion and future perspective

In this study, we analyzed the foraging activity of ants (*Camponotus japonicus*) in five monodomous colonies. The data consisted of daily counts of the passage events of each ant between a nest chamber and a foraging arena. We developed a successful mathematical model based on time series data of foraging worker ants.

Future research should focus on examining the changes in the probability distribution when the number of worker ants included in the study is intentionally increased or reduced. Given the data, it is possible to answer questions such as 1) whether there is a mechanism to control the activity of worker ants so that SDPEC remains at a log-normal distribution if any worker ants are removed from the colony, or 2) what kind of correlation matrix structure is sufficient to cause the distribution of  $N_t$  to be log-normal.

We provided a few explanations to link the experimental results and biological interpretations; another future research avenue is to further examine these links. Since our dataset consists of daily foraging frequency, we could not verify the explanations, therefore a more detailed dataset may prove helpful in this regard.

Moreover, it would be interesting to investigate the advantages of a colony in which SDPEC follows a log-normal distribution. The investigation would possibly suggest that it reflects optimal behavior against risks, such as predation.

## Supporting information

**S1 Fig. Total count of daily passage events  $N_t$ .** Each horizontal axis represents the duration of each experiment. (A) Colony: A. (B) Colony: B. (C) Colony: C. (D) Colony: D. (E) Colony: E. (TIF)

**S1 Table. Number of worker ants in each colony.**  
(TEX)

**S2 Table. Passage counts for each colony (A-E).**  
(TEX)

**S3 Table. Summary statistics: Colony A.**  
(TEX)

**S4 Table. Summary statistics: Colony B.**  
(TEX)

**S5 Table. Summary statistics: Colony C.**  
(TEX)

**S6 Table. Summary statistics: Colony D.**  
(TEX)

**S7 Table. Summary statistics: Colony E.**  
(TEX)

## Acknowledgments

The authors wish to thank all the staff at the Global Career Design Center, Hiroshima University and Frontier Research Center, Toyota Motor Corporation for their kind hospitality. In particular, the authors are grateful to Prof. Toshiharu Akino (Applied Entomology Laboratory, Center for Bioresources Field Science, Kyoto Institute of Technology), Yoshiumi Kawamura (Toyota Motor Corporation) and Atsushi Kawamoto (Toyota Motor Corporation) for their technical assistance and for participating in valuable discussions regarding the study.

## Author Contributions

**Conceptualization:** Hiromichi Goko.

**Data curation:** Osamu Yamanaka, Masashi Shiraishi.

**Formal analysis:** Hiromichi Goko, Osamu Yamanaka.

**Funding acquisition:** Masashi Shiraishi, Hiraku Nishimori.

**Investigation:** Hiromichi Goko, Osamu Yamanaka.

**Methodology:** Hiromichi Goko.

**Project administration:** Hiromichi Goko.

**Resources:** Hiraku Nishimori.

**Software:** Osamu Yamanaka.

**Supervision:** Hiromichi Goko.

**Validation:** Hiromichi Goko, Osamu Yamanaka.

**Visualization:** Hiromichi Goko, Osamu Yamanaka.

**Writing – original draft:** Hiromichi Goko, Masashi Shiraishi.

**Writing – review & editing:** Hiromichi Goko, Osamu Yamanaka, Masashi Shiraishi, Hiraku Nishimori.

## References

1. Hölldobler B, Wilson EO, et al. *The ants*. Harvard University Press; 1990.
2. Beshers SN, Fewell JH. Models of division of labor in social insects. *Annual review of entomology*. 2001; 46(1):413–440. <https://doi.org/10.1146/annurev.ento.46.1.413> PMID: 11112175
3. Robinson GE. Regulation of honey bee age polyethism by juvenile hormone. *Behavioral ecology and sociobiology*. 1987; 20(5):329–338. <https://doi.org/10.1007/BF00300679>
4. Robinson GE. Regulation of division of labor in insect societies. *Annual review of entomology*. 1992; 37(1):637–665. <https://doi.org/10.1146/annurev.en.37.010192.003225> PMID: 1539941
5. Nova N, Pagliara R, Gordon DM. Individual Variation Does Not Regulate Foraging Response to Humidity in Harvester Ant Colonies. *Frontiers in Ecology and Evolution*. 2022; 9:756204. <https://doi.org/10.3389/fevo.2021.756204>
6. Mersch DP, Crespi A, Keller L. Tracking individuals shows spatial fidelity is a key regulator of ant social organization. *Science*. 2013; 340(6136):1090–1093. <https://doi.org/10.1126/science.1234316> PMID: 23599264
7. Fujioka H, Abe MS, Fuchikawa T, Tsuji K, Shimada M, Okada Y. Ant circadian activity associated with brood care type. *Biology letters*. 2017; 13(2):20160743. <https://doi.org/10.1098/rsbl.2016.0743> PMID: 28148829
8. Mildner S, Roces F. Plasticity of daily behavioral rhythms in foragers and nurses of the ant *Camponotus rufipes*: influence of social context and feeding times. *PloS one*. 2017; 12(1):e0169244. <https://doi.org/10.1371/journal.pone.0169244> PMID: 28099496



9. Narendra A, Reid SF, Raderschall CA. Navigational efficiency of nocturnal *Myrmecia* ants suffers at low light levels. *PLoS One*. 2013; 8(3):e58801. <https://doi.org/10.1371/journal.pone.0058801> PMID: 23484052
10. Wilson EO. The relation between caste ratios and division of labor in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology*. 1984; 16(1):89–98. <https://doi.org/10.1007/BF00293108>
11. Pinter-Wollman N, Hubler J, Holley JA, Franks NR, Dornhaus A. How is activity distributed among and within tasks in *Temnothorax* ants? *Behavioral Ecology and Sociobiology*. 2012; 66(10):1407–1420. <https://doi.org/10.1007/s00265-012-1396-2>
12. Beverly BD, McLendon H, Nacu S, Holmes S, Gordon DM. How site fidelity leads to individual differences in the foraging activity of harvester ants. *Behavioral Ecology*. 2009; 20(3):633–638. <https://doi.org/10.1093/beheco/arp041>
13. Dornhaus A, Holley JA, Franks NR. Larger colonies do not have more specialized workers in the ant *Temnothorax alpestris*. *Behavioral Ecology*. 2009; 20(5):922–929. <https://doi.org/10.1093/beheco/arp070>
14. Ishii Y, Hasgeawa E. The mechanism underlying the regulation of work-related behaviors in the monomorphic ant, *Myrmica kotokui*. *Journal of ethology*. 2013; 31(1):61–69. <https://doi.org/10.1007/s10164-012-0349-6>
15. Yamanaka O, Shiraishi M, Awazu A, Nishimori H. Verification of mathematical models of response threshold through statistical characterisation of the foraging activity in ant societies. *Scientific reports*. 2019; 9(1):1–8. <https://doi.org/10.1038/s41598-019-45367-w> PMID: 31222162
16. VISWANTHAN G. Levy flight search patterns of wandering albatrosses. *Nature*. 1996; 381:413415.
17. Humphries NE, Weimerskirch H, Queiroz N, Southall EJ, Sims DW. Foraging success of biological Lévy flights recorded in situ. *Proceedings of the National Academy of Sciences*. 2012; 109(19):7169–7174. <https://doi.org/10.1073/pnas.1121201109>
18. Sims DW, Southall EJ, Humphries NE, Hays GC, Bradshaw CJ, Pitchford JW, et al. Scaling laws of marine predator search behaviour. *Nature*. 2008; 451(7182):1098–1102. <https://doi.org/10.1038/nature06518> PMID: 18305542
19. Reyna-Hurtado R, Chapman CA, Calme S, Pedersen EJ. Searching in heterogeneous and limiting environments: foraging strategies of white-lipped peccaries (*Tayassu pecari*). *Journal of Mammalogy*. 2012; 93(1):124–133. <https://doi.org/10.1644/10-MAMM-A-384.1>
20. Viswanathan GM, Buldyrev SV, Havlin S, Da Luz M, Raposo E, Stanley HE. Optimizing the success of random searches. *nature*. 1999; 401(6756):911–914. <https://doi.org/10.1038/44831> PMID: 10553906
21. Codling EA, Plank MJ, Benhamou S. Random walk models in biology. *Journal of the Royal society interface*. 2008; 5(25):813–834. <https://doi.org/10.1098/rsif.2008.0014> PMID: 18426776
22. de Jager M, Weissing FJ, Herman PM, Nolet BA, van de Koppel J. Lévy walks evolve through interaction between movement and environmental complexity. *Science*. 2011; 332(6037):1551–1553. <https://doi.org/10.1126/science.1201187> PMID: 21700872
23. Mitzenmacher M. A brief history of generative models for power law and lognormal distributions. *Internet mathematics*. 2004; 1(2):226–251. <https://doi.org/10.1080/15427951.2004.10129088>
24. Sornette D. *Critical phenomena in natural sciences: chaos, fractals, selforganization and disorder: concepts and tools*. Springer Science & Business Media; 2006.
25. Nadarajah S. A review of results on sums of random variables. *Acta Applicandae Mathematicae*. 2008; 103:131–140. <https://doi.org/10.1007/s10440-008-9224-4>
26. Robinson EJ, Richardson TO, Sendova-Franks AB, Feinerman O, Franks NR. Radio tagging reveals the roles of corpulence, experience and social information in ant decision making. *Behavioral Ecology and Sociobiology*. 2009a; 63(5):627–636. <https://doi.org/10.1007/s00265-008-0696-z>
27. Robinson EJ, Feinerman O, Franks NR. Flexible task allocation and the organization of work in ants. *Proceedings of the Royal Society of London B: Biological Sciences*. 2009b; p. rspb20091244.
28. Robinson EJ, Feinerman O, Franks NR. Experience, corpulence and decision making in ant foraging. *Journal of Experimental Biology*. 2012; 215(15):2653–2659. <https://doi.org/10.1242/jeb.071076> PMID: 22786642
29. Robinson EJ, Feinerman O, Franks NR. How collective comparisons emerge without individual comparisons of the options. *Proceedings of the Royal Society B: Biological Sciences*. 2014; 281(1787):20140737. <https://doi.org/10.1098/rspb.2014.0737> PMID: 24920474
30. Gardiner CW, et al. *Handbook of stochastic methods*. vol. 3. Springer Berlin; 1985.
31. Wooldridge JM. *Introductory econometrics: A modern approach*. Cengage learning; 2015.



32. Cole BJ. Short-term activity cycles in ants: age-related changes in tempo and colony synchrony. *Behavioral ecology and sociobiology*. 1992; 31:181–187. <https://doi.org/10.1007/BF00168645>
33. Cole BJ, Trampus FI. Activity cycles in ant colonies: worker interactions and decentralized control. *Information processing in social insects*. 1999; p. 289–307. [https://doi.org/10.1007/978-3-0348-8739-7\\_16](https://doi.org/10.1007/978-3-0348-8739-7_16)
34. Hunt ER, Baddeley RJ, Worley A, Sendova-Franks AB, Franks NR. Ants determine their next move at rest: motor planning and causality in complex systems. *Royal Society Open Science*. 2015; 3(1):150534. <https://doi.org/10.1098/rsos.150534>