Paper:

## Influence of Labor Conditions and Interaction Among Individuals on Circadian Activity Rhythms in the Ant *Camponotus Japonicus*

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In this study, we investigated the relationship between the activity rhythms of Camponotus japonicus worker ants and their interactions. Specifically, one or two workers collected from either inside or outside the nest in a breeding colony were placed in a measurement system under a constant dark condition, and their activity rhythms were measured for 14 days. We thereby examined the relationship between the activity rhythm in the system and the experimental conditions, which consisted of four different combinations of working locations during breeding (in/outside the nest) and single/double workers (one ant / two ants) in the measurement system, over a total of 96 samples. A large number of the sampled ants (about 90% of the total) showed circadian activity rhythms. The proportion of circadian activity rhythm was lower and the dispersion of the period was larger in the circadian activity rhythm observed in single workers collected from within the nest than in the other three experimental conditions. In all four experimental conditions, the amplitude of the circadian activity rhythm decayed on an approximate 5-day scale. These results provide quantitative evidence that the activity rhythm of ants is determined by the location of labor and individual interactions during breeding.

Keywords: circadian rhythm, ant, social interaction

## 1. Introduction

Social insects, such as ants, maintain high productivity and a stable social structure as a colony via the complex division of labor to various roles among workers [1, 2]. The sophisticated organization of social insects has been applied to robotics in the form of the idea of swarm robotics or swarm intelligence. In swarm robotics, the aim is to construct a system with high productivity beyond the simple sum of the functions of each element

(robot) through a process whereby relatively simple elements gather and interact appropriately according to the situation. Another goal of swarm robotics is to build artificial systems that realize the characteristics of social insects: i) robustness to damage of some elements, ii) expression of equivalent functions independent of the number of elements, and iii) flexibility to respond to various environmental factors and task demands [3]. In this sense, elucidation of the mechanisms of organization formation and maintenance in social insects is closely related to the progress of robotics. In particular, the mechanism of autonomous role sharing within ant and bee colonies has been applied to swarm robotics algorithms in combination with evolutionary algorithms [4, 5]. In an ant colony, no specific small number of individuals shows leading behavior. Roles are autonomously assigned by direct contact between individuals [6], mouth transfer of food [7], and secretion and response to chemical substances common in the colony [8], enabling organizational behavior of the colony as a whole [7]. In addition, the overlap of activity time periods among multiple workers is also an important factor for the emergence of organizational behavior, and the activity rhythms of workers in environments where light and dark fluctuate during the diurnal cycle or where light is maintained at a constant level have recently attracted attention. For example, the spontaneous behavior of intermediate-size solitary workers of Camponotus compressus, a species of carpenter ant, was maintained in a 24-hour nocturnal or diurnal cycle in a 24-hour light-dark switching condition. However, after transition to a constant dark condition, they underwent various processes such as behavioral shortening, prolongation, or phase shifts depending on whether they were nocturnal or diurnal. In a colony of Camponotus rufipes, a species of carpenter ant, foraging workers maintained a circadian activity rhythm in the presence of food but lost it in its absence. On the other hand, it was found that brood-rearing workers that were forced to be constantly active for 24 hours owing to the presence of immature individuals and that did not show a circadian ac-



Journal of Robotics and Mechatronics Vol.33 No.3, 2021

tivity rhythm started to exhibit such a rhythm when isolated [10]. The reason for this is that the social role of the workers and the associated stimuli from the external environment are known to regulate the activity rhythm, and it has been suggested that the control of the activity rhythm contributes to the optimization of activities throughout the colony [10]. In addition, when young nurse workers of Diacamma sp. worked alone, they exhibited a circadian activity rhythm. However, they tended to be active continuously for 24 hours in the presence of immature individuals (e.g., larvae). This is a reasonable activity pattern considering their role of constant caretaking of immature individuals vulnerable to external stimuli [11]. As shown above, the relationship between the working conditions of individual workers and their activity rhythms is becoming clearer, but there is still much room for progress in elucidating the effects of individual interactions among multiple workers on the activity rhythms of individual workers.

Recent studies showed that young workers of Diacamma sp. exhibited daily cyclical activity both alone and in groups, while older workers exhibited cyclical activity alone but lost periodicity of activity in groups [12]. In an experimental system consisting of one or two workers of Camponotus fellah isolated from the colony, it was reported that the survival of the workers was longer in the isolated experimental system with two workers [13]. Workers of Camponotus rufipes have been shown to have different survival rates after being isolated, depending on the task (brood-care/foraging) in the colony [10]. The authors examined the daily frequency of foraging behavior of Camponotus japonicus workers and showed that the correlation in the frequency of participation in foraging behavior among individuals in a population was maintained on a one-month scale [14]. There was a correlation between the age in days of workers and their location in the nest. As the age in days increased, the workers were more likely to be located further out in the nest, and the frequency of contact between younger individuals was more frequent than that of contact between older individuals [6]. In addition, when workers of Camponotus paris working outside the nest came into contact with ants inside the nest, the circadian activity rhythm of the workers inside the nest was synchronized. It has been reported that the phase (daytime/night) of the circadian activity rhythm of the workers in the nest differs depending on whether the contact is made with only a single worker in the nest or with multiple workers and queens in the nest [15]. To examine the correlation of the activity rhythms among multiple workers and the relationship between the activity rhythms of each worker and its role in the colony, based on these previous studies, we collected workers from inside and outside a nest of a Camponotus japonicus colony with a 24-hour light and dark cycle. We also measured daily activity rhythm, namely circadian activity rhythm, under the constant dark condition.

## 2. Method

### 2.1. Species and Rearing Conditions

A colony of Camponotus japonicus was collected in the Higashi-hiroshima Campus of Hiroshima University. The collected colony was kept in a breeding container consisting of a nest box (150 mm  $\times$  81 mm  $\times$  24 mm) and a foraging space (242 mm  $\times$  306 mm  $\times$  103 mm). The surface of the nest box was wrapped with duct tape to block out light, and the bottom of the interior was covered with plaster. The nest box and the foraging space were connected by rubber tubes to allow the ants to move around. The colony consisted of more than 100 workers and contained a queen ant. The breeding case was placed in a dark room. In the dark room, illumination was provided using white LED lights from 8:00 to 20:00 every day. The laboratory was maintained at a room temperature of 25°C and humidity of at least 30%. In the foraging space, 1 mol/L sugar water was supplied three times a week, and six mealworms were given twice a week.

## 2.2. Experimental Set-Up

The measurement system for measuring the activity of individuals consisted of two tubes of 2 cm in outer diameter cut to a length of about 10 cm and a tube of 1 cm in outer diameter cut to a length of about 5 cm, with an infrared sensor attached to the central tube of 1 cm in outer diameter. The gaps between the tubes were filled with Kimwipes, and one side of the tubing was plugged with a Kimwipe immersed in a water tank to ensure a constant supply of water, while the other was plugged with a dry Kimwipe. For measurement, we used Arduino to record the time when a worker passed under the infrared sensor.

A worker passing under the sensor was considered active. This was called the activity measurement system, and the measurement data were referred to as passage time data. In the experiment, the activity measurement system was placed in an incubator for 14-day measurement. The temperature in the incubator was about  $26^{\circ}$ C, and the humidity was kept to 60%-80%.

## 2.3. Definition of Ants Used in the Experiment and Experimental Method

To examine the correlation between different working conditions and activity rhythms, workers were collected from the nest box or the foraging spaces in the breeding container and placed in the activity measurement system described above to measure daily activity rhythms, i.e., circadian activity rhythms, under constant dark conditions. There were four patterns of placing workers in the activity measurement system (hereinafter, "experimental conditions"): a single worker collected from the nest box ("single in nest"), a single worker collected from the foraging space ("single outside nest"), two workers collected from the nest box ("pair in nest"), and two workers collected from the foraging space ("pair outside nest"). The number of samples in each experimental condition was 27 for single in nest, 25 for single outside nest, 26 for pair in nest, and 17 for pair outside nest. All samples were taken from the same colony. However, the infrared sensor only judged whether an ant passed the sensor and could not identify individual ants. Therefore, in the pairs experiment, we treated the entire passage time data for a pair of ants as a single sample for the analysis. In this study, workers were randomly sampled from inside and outside the nests to collect experimental workers from the colony, and the worker size was not taken into account.

## 2.4. Data Collection and Analysis

The obtained passage time data of the workers were converted into the number of activity passages per unit time, and this was defined as count data. The first 48 hours after the workers were taken out of the breeding container and started to be measured in the observation system were excluded from the data analysis because of the extreme increase in activity, which was considered to be caused by the sudden environmental change. We used ActogramJ (version 1.0) [16] to perform the periodicity analysis on the count data using the chi-square periodogram method. Autocorrelation function analysis was performed on the count data with 1 hour as the unit time, and the periodicity analysis was performed on the count data with 6 minutes (0.1 hour) as the unit time. Because the survival rate of workers isolated from a colony decays as the period of isolation increases [13], as a prerequisite for the periodicity analysis, we calculated the time constant of decay to check whether there was any difference in the decay of worker activity among the experimental conditions. First, the count data were smoothed using a 24-hour moving average and fitted with a two-parameter exponential function  $y = \exp(ax + b)$  to calculate  $\tau = 1/a$ , which represents the time constant of decay. The autocorrelation function was calculated to elucidate the basic state of each data, and the temporal correlation of activity was analyzed.

Next, we conducted a periodicity analysis to determine whether the workers continued their cyclic activity after the transition from the 24-hour light-dark cycle during breeding to the activity measurement system under the constant dark condition. In a periodicity analysis, the strength of periodicity is defined as the maximum difference between the chi-square value of each frequency obtained by the chi-square periodogram method with a significance level of p = 0.05 [12], and the strength of periodicity is called "power." The periodicity and power obtained from the frequency analysis were compared among the different experimental conditions to examine the influence of social roles and interactions on the circadian activity rhythm of workers. Figs. 1-4 show the differences between individuals with and without confirmed periodicity.

## 2.5. Statistical Analysis

Feature time for activity decay was estimated by using the curve\_fit function of the scipy and optimize modules in Python 3 (version 3.8). Statistical tests were performed on the Python 3 platform in the statsmodels module (ver. 0.12.2), using the tukey\_hsd function for multiple comparisons, the f\_oneway function for the one-way analysis of variance (ANOVA), and the Bartlett function for the F-test.

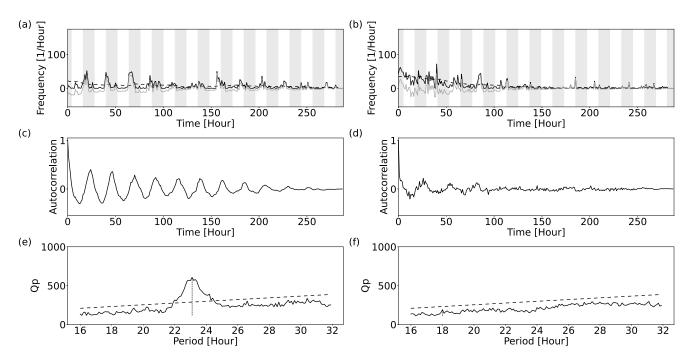
## **3. Experimental Results**

## 3.1. Decay of Activity over Time

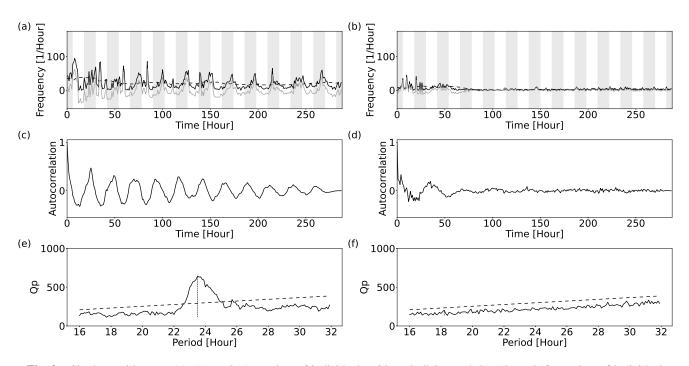
As a result of fitting the time constant of decay  $\tau$ , we found that a decay in activity was observed in many individuals (**Fig. 5**), although there were some cases (n = 2) in which  $\tau$  was negative due to small changes in activity. The average value of  $\tau$  was 4.61 days across all experimental conditions, indicating that the activity level decayed in about 5 days. The results of multiple tests (Tukey HSD) for different experimental conditions did not show any significant difference between any of the experimental conditions. The decay of activity after separation from the colony was considered to be equally expressed in all the experimental conditions.

# **3.2.** Periodicity Analysis and Comparison Between Experimental Conditions

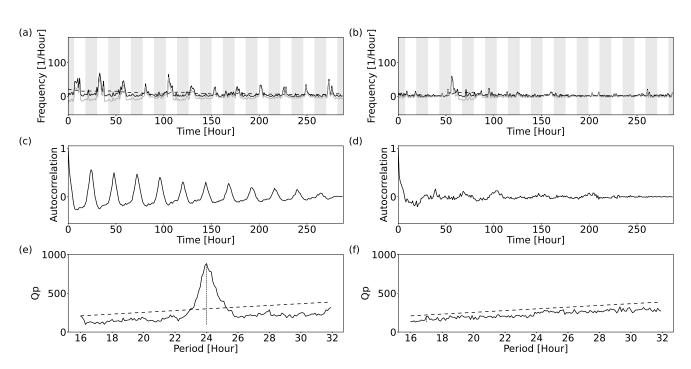
The percentage of samples found to have significant periodicity (chi-square spectrogram, p < 0.05) in each experimental condition is shown in Table 1. In the single in nest condition, 77.8% of the samples had a circadian activity rhythm, and in the other three experimental conditions, more than 90% of the samples had a circadian activity rhythm. The one-way ANOVA for the estimated period of the sample in each experimental condition found to have periodicity (Fig. 6) revealed no significant difference among the experimental conditions (p = 0.66). In addition, when the Tukey-Kramer method was used as a paired comparison multiple test to compare the estimated period and its power among the experimental condition groups, no significantly different (p < 0.05) combinations were noted. However, because the estimated period of the single in nest had a wide distribution of values (Fig. 6), the results of the F-test (Table 2) were relatively significantly different (p < 0.05) for the single outside nest and significantly different (p < 0.05) for the pair outside nest. The results of the test between the single outside nest and the pair in nest also showed a tendency to be different (p = 0.0587). The other combinations of experimental conditions did not produce values that showed significant differences (Table 2). The percentage of samples judged to have a periodicity was low (77.8%) only in the single in nest condition, but the ANOVA for the estimated periodicity of power (Fig. 7) showed no significant difference (p = 0.66), indicating no difference in the percentage of samples with periodicity among the experimental conditions. Fig. 8 shows the relation between the estimated period and its power. There was a tendency for many samples to show high power for the estimated period around



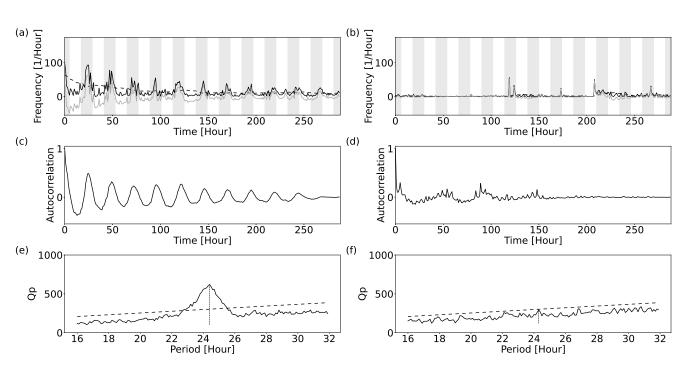
**Fig. 1.** Single in nest: (a), (c), and (e) are data of individuals with periodicity, and (b), (d), and (f) are data of individuals without periodicity. In (a) and (b), the black line is the count data, the gray line is the data with the trend subtracted, and the dash line is the trend. The shading in the background indicates the 24-hour light-dark cycle (gray is light-on time, white is no-light time) in the breeding environment prior to isolation in the constant dark condition. (c) and (d) are autocorrelation functions. (e) and (f) are the values estimated by the chi-square spectrogram method. The straight dash line indicates the significance level of p = 0.05.



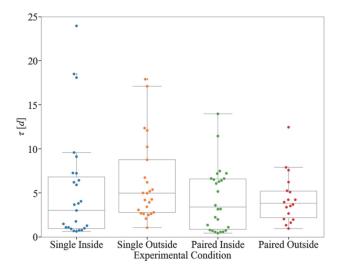
**Fig. 2.** Single outside nest: (a), (c), and (e) are data of individuals with periodicity, and (b), (d), and (f) are data of individuals without periodicity. In (a) and (b), the black line is the count data, the gray line is the data with the trend subtracted, and the dash line is the trend. The shading in the background shows the 24-hour light-dark cycle (gray is light-on time, white is no-light time) in the breeding environment prior to isolation in the constant dark condition. (c) and (d) are autocorrelation functions. (e) and (f) are the values estimated by the chi-square spectrogram method. The straight dash line indicates the significance level of p = 0.05.



**Fig. 3.** Pair in nest: (a), (c), and (e) are data of individuals with periodicity, and (b), (d), and (f) are data of individuals without periodicity. In (a) and (b), the black line is the count data, the gray line is the data with the trend subtracted, and the dash line is the trend. The shading in the background shows the 24-hour light-dark cycle (gray is light-on time, white is no-light time) in the breeding environment prior to isolation in the constant dark condition. (c) and (d) are autocorrelation functions. (e) and (f) are the values estimated by the chi-square spectrogram method. The straight dash line indicates the significance level of p = 0.05.



**Fig. 4.** Pair outside nest: (a), (c), and (e) are data of individuals with periodicity, and (b), (d), and (f) are data of individuals without periodicity. In (a) and (b), the black line is the count data, the gray line is the data with the trend subtracted, and the dash line is the trend. The shading in the background shows the 24-hour light-dark cycle (gray is light-on time, white is no-light time) in the breeding environment prior to isolation in the constant dark condition. (c) and (d) are autocorrelation functions. (e) and (f) are the values estimated by the chi-square spectrogram method. The straight dash line indicates the significance level of p = 0.05.



**Fig. 5.** Distribution of the time constant of decay  $\tau$  under each experimental condition, where the horizontal axis indicates the experimental conditions, and the vertical axis is the time constant of decay obtained by fitting an exponential function to the moving average data of the count data. The number of samples, from left to right, are 27 for single in nest, 25 for single outside nest, 26 for pair in nest, and 17 for pair outside nest.

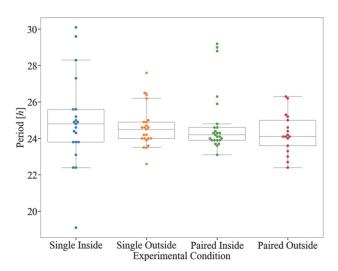
**Table 1.** Percentage of individuals showing periodicity as a circadian activity rhythm. The numerator of the fraction in parentheses is the number of samples with periodicity, and the denominator is the total number of samples.

	Single in nest	Single outside nest	Pair in nest	Pair outside nest
Ratio of significant peaks	77.8% (21/27)	92.0% (23/25)	96.2% (25/26)	94.1% (16/17)

24 hours in all experimental conditions. In the present experiment, the circadian activity rhythm was relatively stable in many samples.

## 4. Summary and Discussion

The activity rhythms of one or two *Camponotus japonicus* workers collected inside or outside the nest in a breeding colony were measured under a constant dark condition, and the presence or absence of a circadian activity rhythm was investigated by a periodicity analysis using the chi-square periodogram method. In all four experimental conditions (single in nest / pair in nest / single outside nest / pair outside nest), most of the samples showed a clear circadian activity rhythm, but the amplitude of the activity rhythm tended to decay on a time scale of about 5 days, in most cases, or 4.61 days, on average, over all experiments. A previous study [13] analyzed the time course and survival rate after isolation. However,



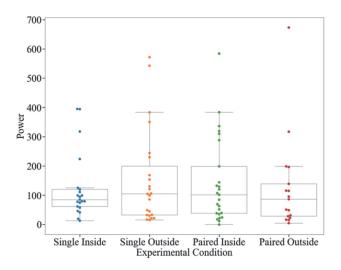
**Fig. 6.** Estimated period under each experimental condition, where the horizontal axis indicates the experimental conditions, and the vertical axis is the estimated period obtained by estimating the period using the chi-square spectrogram method. The number of samples, from left to right, are 21 for single in nest, 23 for single outside nest, 25 for pair in nest, and 16 for pair outside nest.

**Table 2.** *p*-values of the two-group F-test of power and period obtained via the periodicity analysis using the chisquare spectrogram method under each experimental condition. \*\* and \* denote  $p \le 0.05$  and 0.05 , respectively.

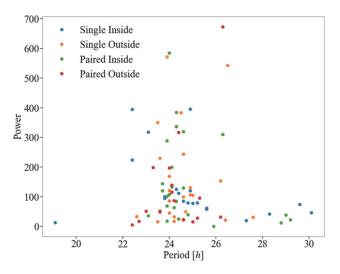
	Period	Power
Single in nest – Single outside nest	0.000729**	0.068472*
Single in nest – Pair in nest	0.091400*	0.202581
Single in nest – Pair outside nest	0.001974**	0.110269
Single outside nest – Pair in nest	0.058271*	0.573798
Single outside nest – Pair outside nest	0.905733	0.932476
Pair in nest – Pair outside nest	0.071175*	0.669340

few studies have reported changes in the amount of activity during worker survival, and the details are not known. The results of this study showed that the circadian activity rhythm itself can be maintained, even when the number of activities declines over time.

The proportion of individuals without a circadian activity rhythm tended to be higher in the experiment with a single ant collected in the nest than in the other conditions, and the variance of the period of circadian activity rhythm was also larger than in the other experimental conditions. These results suggest that the expression of circadian activity rhythms in *Camponotus japonicus* is affected by daily work locations (i.e., work locations in the pre-



**Fig. 7.** Power of estimated period under each experimental condition, where the horizontal axis indicates the experimental conditions, and the vertical axis shows the distance between the spectral peak and the significance level of the period estimated by the chi-square spectrogram method. The number of samples, from left to right, are 21 for single in nest, 23 for single outside nest, 25 for pair in nest, and 16 for pair outside nest.



**Fig. 8.** The relation between the estimated period and its power, where the horizontal axis is the estimated period by the chi-square spectrogram method, and the vertical axis is the power corresponding to the estimated period. The power of the samples with values around the 22–26-hour period was high, indicating that the circadian activity rhythm was well represented.

experimental breeding environment) and by interactions with nest mates during the experiment.

The remaining problem is as follows. In this experiment, we did not account for polymorphism in the *Camponotus japonicus* worker's body size. Therefore, it is necessary to clarify the relationship between the size of the worker's body and the dependence of the worker's work location.

Similar to the results of the present experiment, it has been confirmed in experiments with the Diacamma sp. that the circadian activity rhythm of workers under constant light is influenced by their nest mates, and, in particular, that phase entrainment of the circadian activity rhythm occurs among multiple individuals [12]. The high frequency of expression of the circadian activity rhythm in the present two ant study also suggests mutual entrainment of activity rhythm between individuals. However, among the four experimental conditions described above, the case of a single ant collected from the inside of the nest was markedly different from the others, and it is not possible to determine at this point in the analysis whether this peculiarity originated primarily from the singularity of the population, depended on the work location (work inside the nest) before the experiment, or depended equally on both. In addition, although age in days was not confirmed in the present experiment, it is widely known that the location of work is also correlated with age in days. For example, interaction among old individuals in *Diacamma* sp. has been reported [12], and the measurement and analysis of circadian activity rhythm in consideration of age in days should be addressed in future research.

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Journal of Robotics and Mechatronics Vol.33 No.3, 2021

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