Original article

Effect of constant and fluctuating temperature on the circadian foraging rhythm of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae)

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ABSTRACT

Understanding circadian foraging rhythms activity of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae) foragers at different temperatures is an important step towards developing control measures in Integrated Pest Management (IPM) programs. In this study, the circadian foraging rhythm activities of *S. invicta* foragersat different temperature were investigated under laboratory and field conditions. Results indicated that the foraging activity increased after sunrise, and maximum foraging occurred at 14:00 (foraging rate was 69.22 ± 0.57 and 72.58 ± 1.15 foragers/min in the first and second year, respectively) in the tea fields of Guangzhou during autumn. Furthermore, foragers demonstrated circadian rhythms and exhibited a unimodal after 24 h. A significant correlation was found between foraging activity and temperature. *S. invicta* colonies were active at moderate soil temperatures (approximately 26.65 °C to 29.24 °C). The preferred temperature of the colonies was 26 °C, followed by 22 °C and 18 °C in the laboratory. The individual *S. invicta* activity was maximum at 17:00 (18.67 ± 1.66 times /10 min) and minimum at 5:00 (8.33 ± 2.51 times/10 min) at 26 °C. The fluctuating temperature had a significant impact on individual locomotor activity ($r = 0.8979$, $P < 0.01$) but did not alter the rhythm activity. Our results demonstrated that temperature might play an important role in circadian foraging rhythms activity of *S. invicta*. These results may have implications for the development of more effective fire ant management strategies.

1. Introduction

Solenopsis invicta Buren (Hymenoptera: Formicidae) commonly called red imported fire ant, most notorious pest and has invaded more than 20 countries, e.g., Australia, China, Taiwan, India, Japan, South Korea, Myanmar, Laos, and Vietnam (Allen et al., 1994; Vinson, 1997; Wang et al., 2019). In China, *S. invicta* is considered a most notorious ant species and have been invaded more than 15 provinces in China (Zheng and Zhao, 2005; Huang and Huang, 2010; Wang et al., 2019; Zeng et al., 2005; Ma et al., 2018; Wang

et al., 2019). The foraging activity of *S. invicta* has two annual peaks in Guangdong, China (Li et al., 2008; Jiang et al., 2011). Daily foraging activity depends on colonies' strength (Chen et al., 2010). Global warming is also the main reason to influence the *S. invicta* colonies trend over the past 20 years throughout China (Yu et al., 2011). The *S. invicta* are invading their strength towards the northern areas (Hickling et al., 2006; Robinet and Roques, 2010; Kwon et al., 2014; Wang et al. 2019). However, the potential northern boundary of natural expansion for fire ants in China is much less clear (Xue et al., 2005; Zhou, 2005; Chen et al., 2006; Du et al., 2007).

Abiotic factors including light (Narendra et al., 2010; Stieb et al., 2012), soil moisture (Kaspari and Weiser, 2000; DiGirolamo and Fox, 2006; Menke and Holway, 2006), and temperature (Cerdá et al., 1998; Cole et al., 2010; Jayatilaka et al., 2011) have a great impact on the foraging activity of *S. invicta* colonies. Temperature and rainfall considered the key factors that help determine the geographical distribution and invasion of *S. invicta* (Korzukhin et al., 2001; Morrison et al., 2004). The effects of seasonal temperatures on *S. invicta* foraging activity was studied in Florida (Porter and Tschinkel, 1987). Similarly, the foraging activity of *S. invicta* in Central Texas at different temperatures (10–50 °C) (Drees et al., 2007). Low temperatures have a strong effect in making slow foraging activity in *S. invicta* foragers (Porter and Tschinkel, 1987). *S. invicta* colonies can survive in to cooler regions (Vogt et al., 2003).

Entomopathogenic fungi e.g., *Beauveria* sp., *Metarhizium* sp. are effective biocontrol agents against *S. invicta* (Wang et al., 2010; Lü et al., 2011; Qiu et al., 2014). Similarly, under Integrated Pest Managements (IPM) circadian clocks techniques are very important to understand the behavior of social insects e.g. *S. invicta* for their safer control measures (Frisch and Koeniger, 1994; Moore, 2001). Studies on the foraging activity of *S. invicta* in responses to different temperatures accompanying seasonal or regional variations in China have not been measured.

Considering the importance of temperature fluctuation, in the current study, circadian rhythms activity of *S. invicta* (in colonies and individual level) was observed at constant and fluctuating temperatures. We used a video-computer recording system to record and analyze the circadian rhythms of foraging at different temperatures. We attempted to characterize the daily foraging rhythm of *S. invicta* in the tea field located in Guangzhou, Guangdong, China. The potential relationships between foraging activity and temperature fluctuation were observed. Three different temperatures (18 °C, 22 °C, and 26 °C) were tested on colonies reared in the laboratory. Studies at individual level were conducted to determine whether foragers demonstrated internal rhythms under constant or fluctuating temperatures. This study will provide solid data for the timing of insecticidal bait applications to take advantage of foraging rhythm, which will be appropriate in more southern portions of the fire ant range in China.

2. Materials and methods

2.1. Source colonies and experimental nests

Colonies of *S. invicta* were collected from different District in Guangzhou, China (23°06′ N, 112°12′ E). All colonies were polygyne form. Colonies were maintained in the laboratory according to the methodology of Lei et al., (2019).

2.2. Daily foraging activity in the field

Field research was conducted in a tea plantation at Baiyun, during the autumn season (September–November) in 2018 and 2019.

This plantation had not been subjected to fire ant control, and tea bushes had not been exposed to pesticides in the field. Field works were conducted in the autumn season, which featured large temperature differences; this was because a previous study showed a peak in the trapping number of *S. invicta* in Guangzhou during the autumn season (Liu et al., 2016). Three colonies (20 cm diameter and 15 cm high, 30 cm diameter and 20 cm high, 40 cm diameter and 25 cm in length) were selected randomly; the distance between each colony was greater than 10 m. Colony size was estimated from the mound volume (Tschinkel, 1993). We then searched for the nest entrance close to the ant mound; usually, the nest entrance is located within a 3.5 m radius of the ant mound. Foraging trails could be found leading away from the nest. Foragers were allowed to re-form their foraging trail for 20 min prior to the recording. The trails were under sunshade cover (the diameter of the sunshade surface was 3 m) to protect it from direct exposure to sunlight and rain (Fig. 1A). The three colonies were observed on the same day to minimize variation in weather conditions between days.

To be able to monitor the complete foraging activity of individual ants, a video-computer recording system (VCRS) was used. A camera (BL-C3QA720PL, Shenzhen Wave-particle Technology Co., Ltd., China) was mounted to a tripod and placed close to the foraging trail (Fig. 1A). The camera automatically recorded the date and time when workers passed the focal area. Night monitoring was carried out using an infrared lamp ($\lambda > 600$ nm). To examine how environmental temperature affects foraging activity, the maximum temperature was recorded up to a level of ±0.21 °C using Onset data loggers (HOBO® Data Loggers U23-003, One Temp Pty., Ltd., Australia). To record air temperature, the logger was used. Soil temperature at a depth of 2 cm was recorded using the logger to represent the temperature of the foraging trail (Porter and Tschinkel, 1987). The loggers were set to record temperature with 1 min intervals and allowed to run for 6 days. Data were copied from the camera and logger daily.

2.3. Experiment I. Effects of constant temperature on daily colony foraging activity

Three experimental colonies were used, each consisting of five or more queens, approximately 2000 workers, and 30 larvae or pupa. Constant daily mean temperatures were set to 26 °C, 22 °C, and 18 °C. To examine the effect of different temperatures upon foraging intensity, colonies were placed in 3 temperature-controlled rooms and exposed to 26 °C continuously for 5 days, which was then changed to 26 °C, 22 °C, and 18 °C continuously for 5 days, separately. There were three replicates per temperature treatment, and a new colony was used for each replicate. Ants crossing the tube to the foraging area were automatically recorded by VCRS (Fig. 1C). The mean number of workers passing the trail every 5 min for 1 h on three consecutive days was counted in each colony.

2.4. Experiment II. Effects of fluctuating temperatures on daily individual locomotor activity

This experiment was designed to determine the impact of temperature on individual locomotor activity in *S. invicta*. Medium-sized worker ants (*medias*, head width (1.0–1.3 mm)) were selected for these experiments to eliminate the influence of body size on behavior. Workers observed on the food were identified as foragers. CO_2 was used to anesthetized the *S. invicta* for 30 sec and then filtered with two different screens, one with a mesh size of 14 units and the other with a mesh size of 18 units (Shanghai
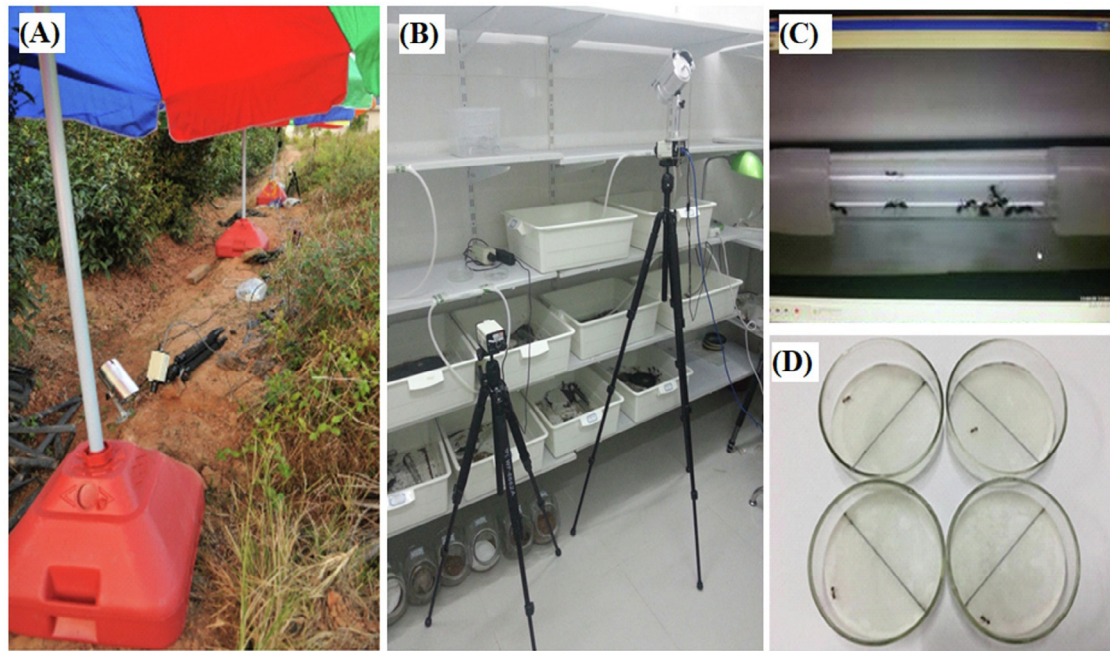
Fig. 1. Monitoring experiments of the activity of *Solenopsis invicta* foragers. (A) Monitoring arrangement in a tea plantation. Foraging trails were observed by cameras and monitored for approximately 5 days. (B) Constant temperature experiment for monitoring the foraging activities of colonies in the laboratory. Colonies of *S. invicta* were given access to a food source in a foraging area linked to the nest by a plastic tube bridge. The camera automatically recorded the date and time when workers passed the focal area, as well as the identity of the passing foragers. (C) A transparent silica tube was used to observe passing foragers. (D) Constant and fluctuating temperature experiment for monitoring individual locomotor activity in the incubator.

Zhenchun Powder Equipment Co., Ltd., China). Majors were retained on the size 18 mesh sieve while minors and medias dropped onto the size 14 mesh sieve; only medias retained on the 14 mesh sieve were kept for experiments while minors dropped and were discarded. The mean ± standard error of the head width in medias was 1.15 ± 0.1 mm (N = 10), which was measured with a microscope (Zeiss, Jena, Germany) fitted with a graticule. Prior to the experiment, workers were deprived of food for 48 h to empty their crops. In this way, each treatment contained workers with approximately the same level of hunger.

The locomotor activity of foragers was monitored individually under the laboratory. Two incubators, which were adjusted to either a constant or fluctuating temperature, were used for all individual experiments. Individual locomotor activity was studied at two sets of constant temperatures e.g. 26 °C ± 0.8 °C and 18 °C ± 0.7 °C, while fluctuating temperatures were 21.10, 21.16, 22.73, 23.65, 24.61, 27.39, 27.98, 27.54, 28.07, 27.19, 26.24, 24.87, 23.57, 23.02, 22.64, 22.69, 22.65, 22.29, 21.96, 21.59, 21.55, 21.49, 20.95, and 20.47 °C with recorded 85 ± 1% RH and a photoperiod of 12:12 h light: dark. We selected 26 °C and 18 °C as a constant temperature to test locomotor performance because it was consistent with the colony treatment above. Petri dishes (30 mm in diameter and 10 mm in height) were used as experimental arenas. Each Petri dish had been treated with Fluon (to prevent workers from escaping). The bottom of each Petri dish was covered with a moistened filter paper. An individual forager was placed into the Petri dish for 6 h before experiments began and allowed to acclimate to the environmental change (Fig. 1D).

After the start of the experiment, foragers were introduced into experimental arenas individually (one forager per arena), and their movements were recorded for 3 consecutive days with a camera. The bottom of each Petri dish was bisected with a simple marked line. We then recorded the number of times a forager crossed the line; this allowed us to assess the locomotor activity of each indi-

vidual. Each treatment (individuals with constant and fluctuating temperature conditions were used as different treatments) was replicated 16 times (i.e., 16 individual foragers).

2.5. Data analysis

For all experiments, activity was calculated by observing the numbers of foragers exposed to the camera. The foraging rate was defined as the number of foragers that passed through a given path per unit of time. Foraging activity was assayed by the foraging rate (Lei et al., 2019). The mean foraging rate index at each time point over 3 days was calculated using the following equation.

$$\text{Foraging rate index} = 100 \times E_t / E_d.$$

where E_t was the mean number of foragers exposed (i.e., moved out from the nest and returned) in the 10 min filming period at each time point, and E_d was the sum value for the 24 time points each day.

For field observations, we recorded air and soil temperature over 24 h. Multiple regression was used to determine the effect of foraging rate to variations in soil temperature.

Individual locomotor activity was quantified by calculating the number of foragers that crossed the middle line. To compare activity patterns between the colony and individuals, the locomotor activity was normalized to the locomotor activity index, which was defined as the mean relative proportion of individual forager crossing times (±SEM) at each time point across foragers over a 24 h period (24 time points). The patterns of individual locomotor activity in constant and fluctuating temperature conditions were analyzed separately. Multiple regression was used to determine the effect of individual locomotor activity under fluctuating temperature. Statistical analyses were performed using SAS 2.1 software (SAS Institute Inc., North Carolina, USA).

Fig. 3. Scatter diagrams and linear regression lines of the correlations between forager activity and temperature. The foraging rate in relation to soil temperature at a depth of 2 cm for the autumn sample of 1st year (A) and the autumn sample of 2nd year (B). Data are from both trials; points and error bars represent means and standard errors, respectively.
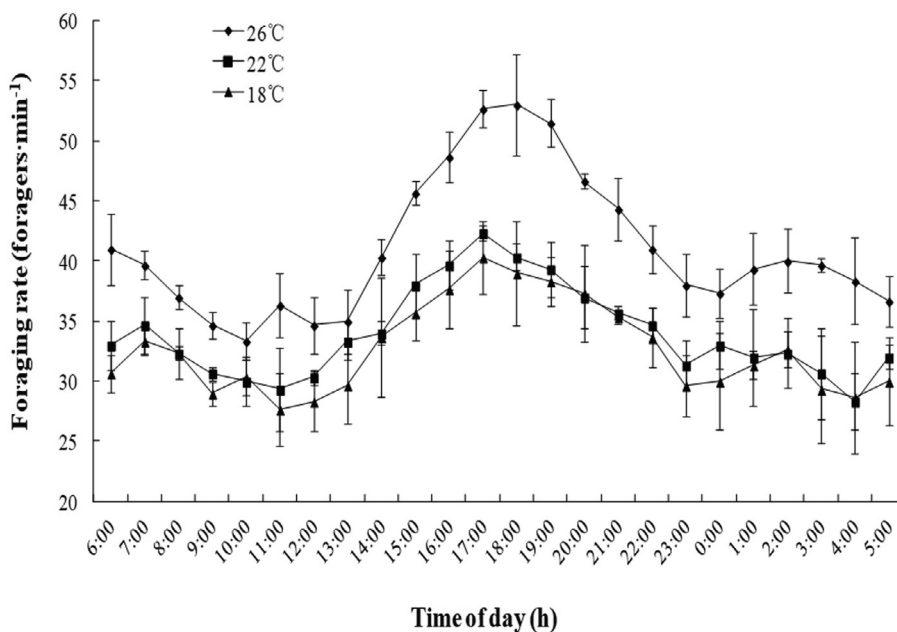
Fig. 4. Foraging rhythm patterns of *Solenopsis invicta* under three constant temperature conditions. Foraging rate for each data point (±SEM) was plotted as the mean values over 24 h and across colonies (n = 3 colonies). Standard error bars were calculated from variation across three colonies.

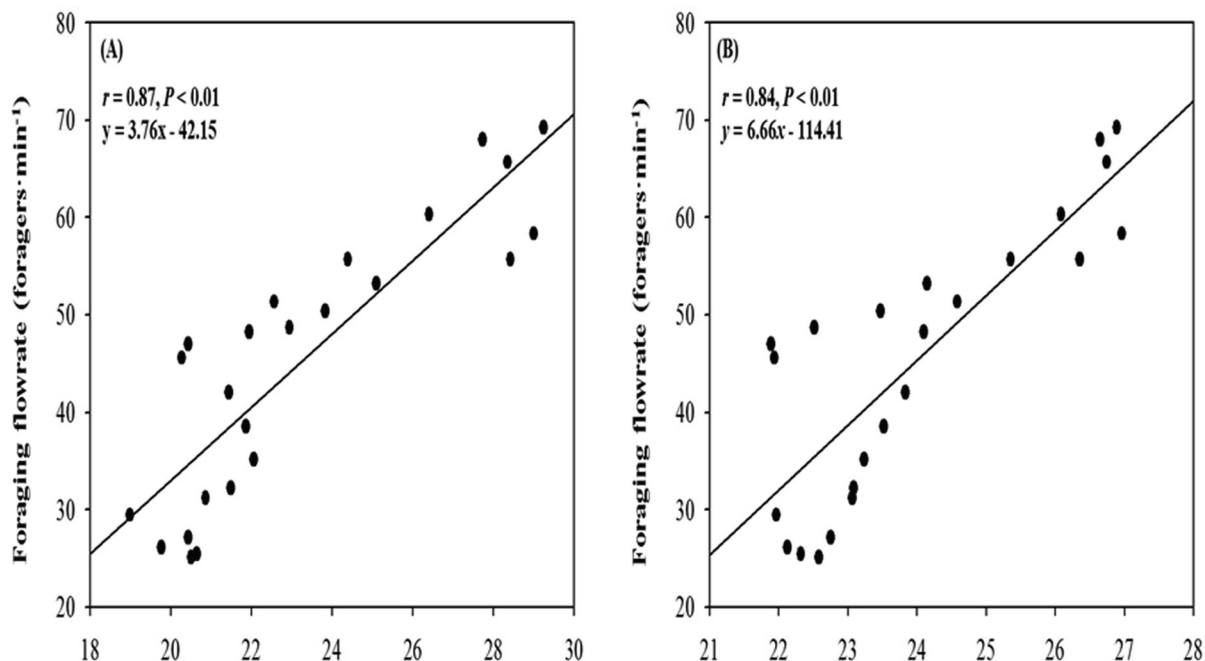22 °C and 18 °C, with common peak activity at 17:00 and minimum activity at 4:00. The most striking difference in terms of activity at the three temperatures was a considerably higher activity at each time point under 26 °C.

3.3. Effects of constant temperature on individual locomotor activity

Foragers exhibited circadian locomotor activity rhythm under constant temperature conditions. This activity showed a multimodal pattern at both 18 °C and 26 °C. The individual activity

was lower at 18 °C than 26 °C. The locomotor activity increased with ambient temperature and reached a maximum value at 17:00 at 26 °C (18.67 ± 1.66 times /10 min) and 18:00 at 18 °C (10.33 ± 1.04 times/10 min), respectively (Fig. 5A).

3.4. Effects of fluctuating temperature on individual locomotor activity

The fluctuating temperature had a strong effect on the individual locomotor activity of *S. invicta*. The activity started at 7:00 and increased significantly until 15:00 (26.75 ± 2.89 times/10 min) per

Fig. 5. Circadian pattern of individual locomotor activity under different temperature conditions: (A) constant 26 °C and 18 °C and (B) fluctuating temperature. Standard error bars were calculated from the variation across replicated individuals.

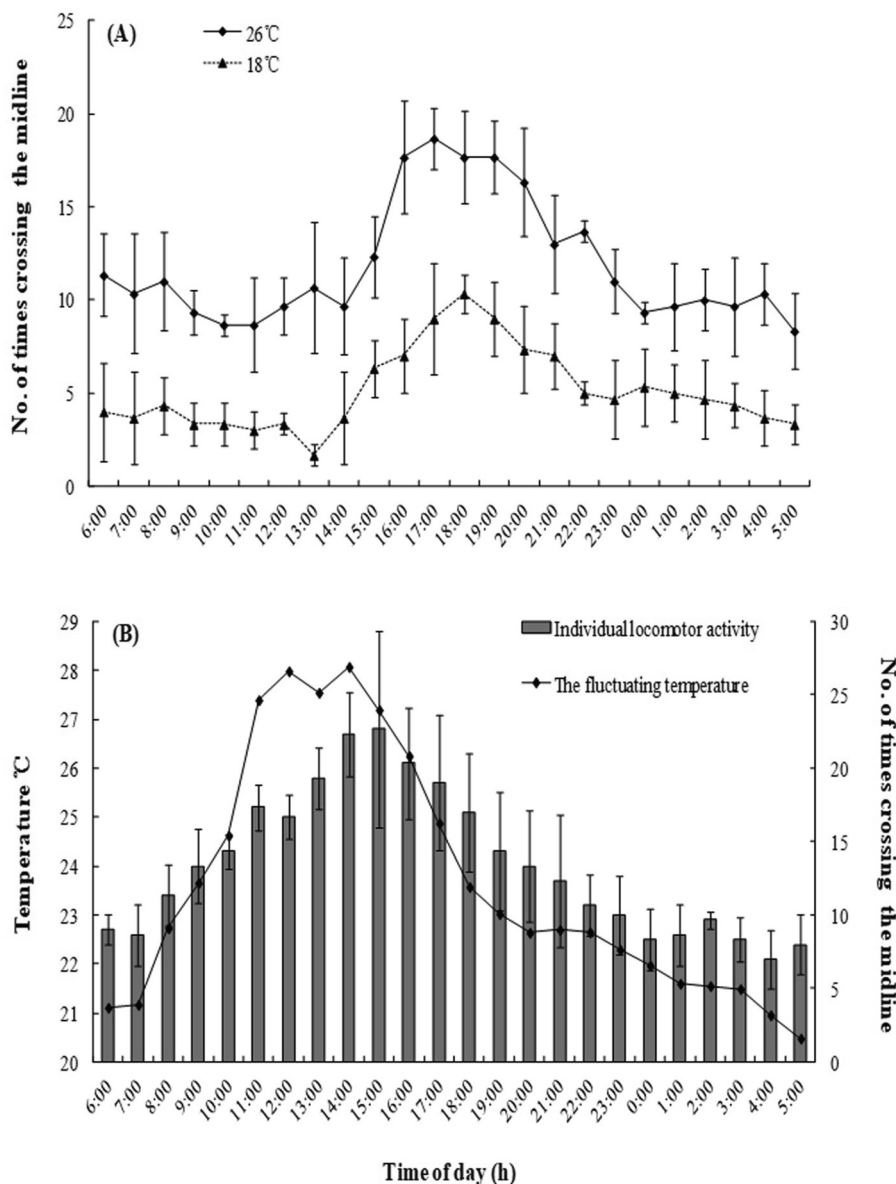day, with the exception of a slight decrease from 11:00 to 12:00. The activity then decreased significantly from 15:00 to 4:00, with the exception of a slight fluctuation from 1:00 to 3:00 (Fig. 5B). There was no difference between colony foraging activity and individual locomotor activity in *S. invicta* foragers exposed to 26 °C (Fig. 6). Similar patterns of activity, at the colony and individual level, were evident with considerable fluctuation between 13:00 and 23:00, with a common peak of activity (17:00 to 18:00).

The locomotor activity appeared to follow a similar pattern to that of temperature throughout the day. Individual locomotor activity changed in accordance with temperature fluctuation. Foragers crossed the line 7–23 times/10 min during the fluctuating temperature regimes from 20.47 °C to 28.07 °C. The fluctuating temperature was significantly correlated with the individual locomotor activity (Fig. 7). A linear relationship was found between individual locomotor activity and temperature: the higher the temperature, the higher the locomotion.

4. Discussion

Ants can adapt to fluctuating temperatures zones (Falibene and Josens, 2014). In both laboratory and field experiments, foraging and individual activity of *S. invicta* were directly proportional to temperature, which showed that environmental temperature might play an important role in the timing of foraging behavior in *S. invicta*.

In Florida, *S. invicta* workers foraging activity were more at night, but neither time of day nor night/day were significantly correlated with foraging rates (Porter and Tschinkel, 1987). However, *Myrmecia pyriformis* ants are known to be nocturnal throughout the year in Canberra (Jayatilaka et al., 2011). In the present study, we showed that *S. invicta* in Guangzhou foraged during the day and night but less in the nights. The *S. invicta* foragers visited food sources in the day, and peak foraging was observed between 12:00 and 14:00. Similarly, *S. invicta* in North Carolina was
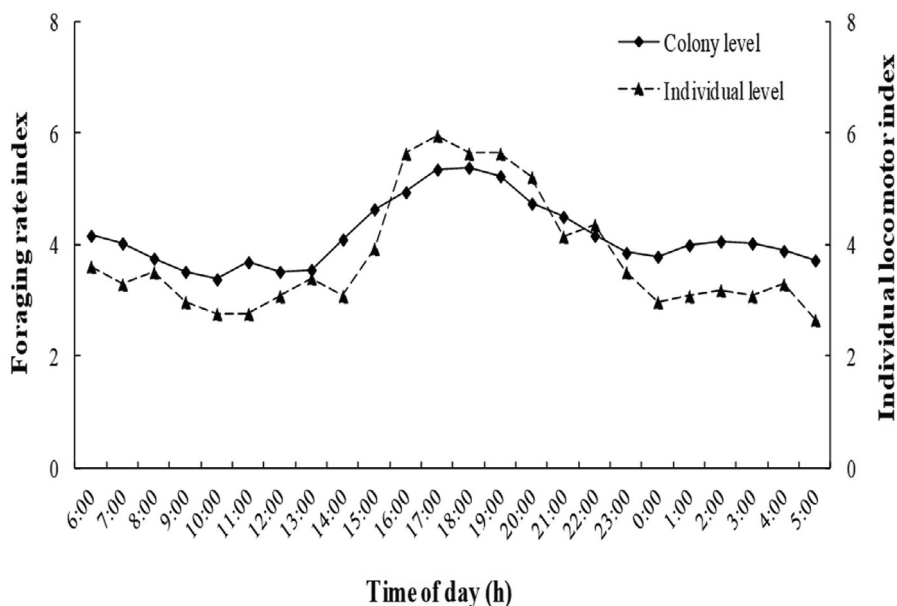
Fig. 6. Circadian activity rhythm patterns of individual *Solenopsis invicta*, compared with colonies, under a constant 26 °C. The foraging rate index for each time point (±SEM) is plotted as mean values across colonies ($n = 3$) while individual locomotor indices are plotted as the mean relative proportion of individual forager crossing times (±SEM) at each time point across foragers ($n = 16$).
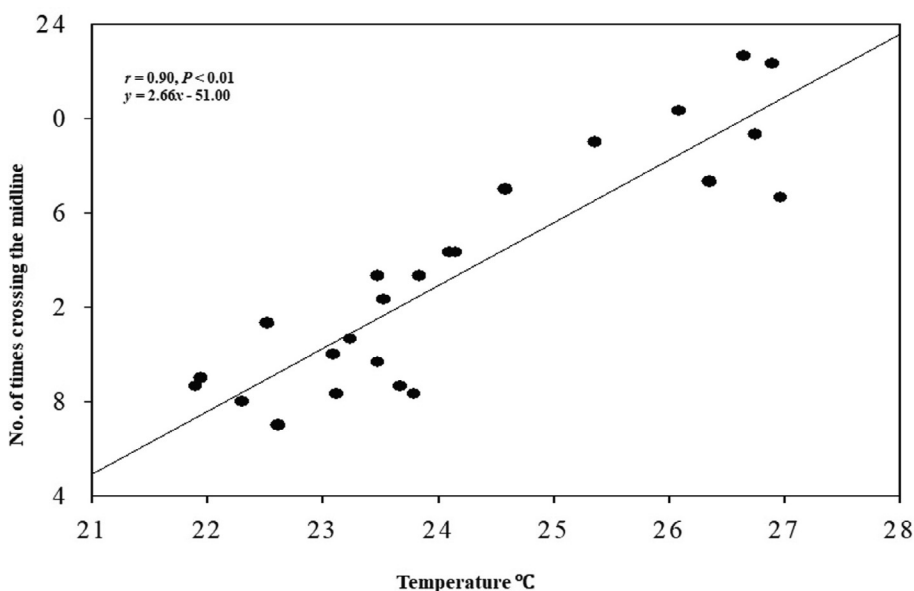

Fig. 7. Correlation between individual locomotor activity and fluctuating temperature. Data points and error bars represent means and standard errors, respectively. A positive relationship was found between these variables.

observed to forage during the day, while in the night, the foraging activity low (Kidd and Apperson, 1984). In the other species of ants, the activity pattern of *Oecophylla smaragdina* was low from 10:30 to 14:00 and peaked was between16:00 and 21:00 (Peng et al., 2012). *Solenopsis geminata* foraging activity was reported maximum at midnight (Norasmah et al., 2006). In our current study, the foraging activity of *S. invicta* demonstrated internal rhythms in the field. The foraging rhythm of *S. invicta* foragers exhibited a unimodal pattern daily, and might play an important role in the management of foraging behavior. *Solenopsis invicta* was sensitive to temperature changes, but workers did exhibit a tendency to forage at night. In contrast, to those published here, the *S. invicta* foragers were most active in the cool areas in the day. However, this

primarily occurred because environmental temperatures surpassed thermal limits for invasive fire ants at the hottest time of the day. There likely exists a seasonal component where foraging activity is maximized at the hottest part of the day in certain months (e.g., fall months in this study) but not in others (e.g., >38 °C when the temperature reached extreme values) which would be useful information to know for management and bait application. This would help to find a better way to control this species of ant. Because these fire ants forage at night, control measures could be deployed during the night to increase the probability of ants contacting the bait.

A previous study showed that low temperatures (15 °C) limited the activity of *Camponotus tonkinus* during the early spring and late

autumn season (Wang and Liu, 1998). In another study, *Myrmecia croslandi* were shown to tune their daily activity to avoid temperatures over 35 °C (Jayatilaka et al., 2011). A narrow range of temperatures (to leave their nest, between 25 °C and 30 °C) was observed in *M. croslandi* colonies, and workers can tolerate high temperatures (Jayatilaka et al., 2011). Previously, it has been demonstrated that the foraging activity of *S. invicta* on soil was most strongly influenced by air and soil temperatures (Kidd and Apperson, 1984). Our current study showed that higher temperatures stimulated the foraging activity of *S. invicta* and that changes in soil temperature synchronized rhythms. According to unimodal activity in the field, *S. invicta* workers come out from the colonies in high temperatures on mid-day. *S. invicta* workers don't prefer the high and low air temperatures, and the preferred active time was reported e.g. 2 h behind the highest daily air temperature time point. These results suggested that workers able to feel high temperatures (using their circadian clocks) (Majercak et al., 1999; Quiring and McNeil, 1987). This would then allow *S. invicta* workers to temporally organize their foraging activity to avoid extremely high or cold temperatures.

Earlier research showed that threshold levels for various types of activity in *Solenopsis saevissima* were uniformly temperature-dependent (Markin et al., 1974). In our current laboratory study, foragers were able to regulate their foraging activity within a narrow temperature range (18 °C to 26 °C). Therefore, the effect of lower temperature on foraging specialization was not particularly strong but was still significant for some aspects in our data set.

Constant temperature caused small phase-shifts in the timing of peak activity levels of *S. invicta* colonies. Peak foraging activity under constant 26 °C was seen at 18:00, which was 4 h later than that found in the field (14:00). However, the maximum foraging rate (69.22 ± 0.57 and 72.58 ± 1.15 foragers/min in 1st and 2nd years, respectively) in our field study was higher than that under constant 26 °C in the laboratory (53 ± 4.16 foragers/min). These results could be attributed to the specific range of experimental temperatures used in our study, or to some traits of *S. invicta* that overcome the stress of temperature variation (from fluctuating natural temperature to manipulated constant temperature). Other environmental factors in the field, including photoperiod changes due to seasonal alterations, potentially have a stronger effect on behavioral thresholds (Shiga, 2013), and also on the crucial transition of workers moving from the nest and undertaking outdoor activities (Jürgen Stelzer et al., 2010). Circadian rhythms produced by a biological clock that synchronized with cycles of light and temperatures (Fan et al., 2007). Eight clock genes have been identified in *S. invicta* that are responsible to identify the expression pattern (Ingram et al., 2012). In *Drosophila*, heat pulses are known to trigger (an association between the clock genes CRY and PER-TIM), which suggests that CRY and PER-TIM also contribute to temperature establishment (Fan et al., 2007). Future work should also determine how the interaction between temperature and photoperiod affects the rhythm of foraging and forager behavior.

In our present study, individual foragers remained active around the clock under both constant and fluctuating temperatures. The rhythmic pattern of foraging activity in the colony was consistent with the locomotor activity observed in *S. invicta* individuals and suggested that individual locomotor (walking) activity may depend on their daily activity rhythms. Peak locomotor activity of individual foragers occurred at 15:00 under fluctuating temperature and was approximately consistent with the peak time point of foraging observed in the field (14:00). Foragers, which probably need to anticipate periodic events in nature precisely, displayed locomotor activity rhythms that were synchronized for 24 h period. Maximum foraging activity occurred at 19:00 in colonies, which was 2 h later than the maximum individual locomotor

activity observed under constant 26 °C conditions (17:00) (Sharma et al., 2004).

The environmental temperature might be one factor with which to fine-tune foraging activity via self-organized patterns among *S. invicta* workers. By modifying temperature experimentally, we provided clear evidence that *S. invicta* does indeed measure temperature and relies on an internal rhythm to begin foraging. Environmental temperature promoted significant changes in foraging behavior. However, more research on the function of foraging-related genes in this ant under different temperature conditions is now required to determine whether such genes in *S. invicta* regulate foraging activity. Our results, even though the expected activity in daily temperature changes, could be more drastic than in our experimental design. Considering the particularities of our very simple biological and physical systems are useful in clarifying the potential consequences of temperature variation in future studies that deals with population dynamics, individual performance, and environmental temperature stress.

Acknowledgments

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