



RESEARCH ARTICLE - BEES

Diurnal Temperature and Time Affect Visitation Patterns of Honey Bees

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Abstract

Temperature is one of the most important environmental factors affecting honey bee activity, while ambient temperature varies widely during the daytime. We speculated that the daily visitation patterns of honey bees were closely related to the time of day and temperature. Our understanding of the effects of ambient temperature and daytime on visitation patterns of honey bees is limited. Here, we surveyed the visitation rate of honey bees (both *Apis cerana* and *Apis mellifera*) to flowers of 14 cultivated species and compared the visitation patterns of honey bees concerning diurnal temperature and time. Our observations suggested that diurnal temperature variation was significantly positively correlated with the visitation rate of honey bees only in three plant species. Honey bees began visiting flowers when the ambient temperature exceeded 16 °C. The optimal temperature range for foraging of honey bees was 38–42 °C. The maximum average temperature occurred between 1300–1400 h, while the optimal visitation time for honey bees was 1400–1500 h, which did not correspond to the maximum average temperature. Our results suggested that the visitation patterns of honey bees were affected by both the time of day and temperature. Honey bees tended to visit more flowers in the noon and afternoon when the temperature was higher than in the forenoon.

Introduction

Honey bees contribute to human diets directly through honey and indirectly by providing pollination services to many crops and wild plants (Potts et al., 2010; Su et al., 2022). The foraging activity of honey bees can dramatically affect pollination and honey production (Aizen & Harder, 2009). Honey bee visitation to flowers depends on a variety of factors, including time of day, ambient temperature, relative humidity, and solar radiation (Burrill & Dietz, 1981; Herrera, 1990; Abou-Shaara, 2014; Abou-Shaara et al., 2017; Nishanthini & Kanagarajan, 2024). However, ambient temperature varies widely during the daytime, which may significantly affect honey bee activity (Arroyo et al., 1985; Herrera, 1990; Cui & Corlett, 2016). To date, our understanding of ambient

temperature and daytime influence on visitation patterns of honey bees is limited.

Temperature is one of the most important environmental factors affecting honey bee activity (Burrill & Dietz, 1981; Nishanthini & Kanagarajan, 2024). Arroyo et al. (1985) concluded that the lower visitation rates of insects to flowers were due to a direct effect of lower average temperatures on insect physiology and behavior at higher elevations in the high Andes of central Chile. Since temperature directly affects foraging rates and insect physiology, comparing insect activity at different temperatures under similar environmental conditions should yield variation in visitation rates (Arroyo et al., 1985). Burrill and Dietz (1981) found that increasing temperatures resulted in increasing honey bee (*Apis mellifera*) flight departures and vice versa. Therefore, we hypothesized



that the visitation rate of honey bees to flowers in a given plant species would increase as temperature increased during the daytime.

In addition, Arroyo et al. (1985) proposed an optimal temperature range for the foraging of insects. Temperatures below the foraging optima probably affected visitation rates by reducing the velocity of flight, rate of warm-up, and ability of an insect to initiate flight (Arroyo et al., 1985; Corbet et al., 1993). At temperatures beyond the optimal foraging, the limiting factor was probably overheating (Heinrich, 1979; Arroyo et al., 1985; Corbet & Huang, 2016; Glass & Harrison, 2024). However, the optimal temperature range for honey bee visitation to flowers remains unknown.

Given that ambient temperature varies with the time of day, it is possible that both the time and temperature affect honey bee visitation to flowers. Herrera (1990) showed that the activity curve of honey bees (*A. mellifera*) exhibited a distinctly bimodal activity pattern, with peaks in the early morning and late afternoon and a marked decrease around midday. It is worth noting that the temperature ranges may be similar in the early morning and late afternoon but different from midday on sunny days. We speculated that the daily visitation patterns of honey bees were closely related to the time of day and temperature, and there must be an optimal visitation time for honey bees, which may correspond to the maximum or average temperature during the daytime if the visitation rate increases with temperature.

Honey bees, including the eastern honey bee *A. cerana* and the western honey bee *A. mellifera*, are generalist visitors who visit a wide range of flower species for floral rewards (Willmer, 2011; Nishanthini & Kanagarajan, 2024). In this

study, we surveyed the visitation rate of honey bees (both *A. cerana* and *A. mellifera*) to flowers of 14 cultivated species and compared the visitation patterns of honey bees concerning diurnal temperature and time. Based on field investigations, we aimed to address the following questions: (1) Does the visitation rate of honey bees to flowers in each plant species increase with diurnal temperature? (2) What is the optimal temperature range for honey bee visitation to flowers? (3) Does the optimal visitation time for honey bees correspond to the maximum average daytime temperature? This study will be helpful for further understanding the effects of ambient temperature and daytime on visitation patterns of honey bees.

Materials and methods

Study sites and species

This study was conducted at two sites: Site 1 on the campus of China West Normal University (30°48'N, 106°04'E; 270 m above sea level) in the northeast of Sichuan Province, and Site 2 on the campus of Anhui Normal University (31°20'N, 118°22'E; 18 m above sea level) in the east of Anhui Province, both in southern China. A total of 14 cultivated plant species (i.e. *Brassica napus*, *Malus halliana*, *Robinia pseudoacacia*, *Trifolium repens*, *Coreopsis basalis*, *Cuphea hookeriana*, *Zinnia elegans*, *Tagetes erecta*, *Hypericum monogynum*, *Nandina domestica*, *Viburnum chinshanense*, *Viburnum awabuki*, *Aesculus chinensis*, and *Campsis grandiflora*; see Table 1) were randomly investigated from March to July in 2023, and from March to May in 2024. All species produce hermaphrodite flowers and grow on open slopes. Although we observed that the flowers of

Table 1. Relationships between diurnal temperature variation and visitation rate of honey bees in 14 flowering species.

Species	Year	Diurnal temperature (°C)			Visitation rate of honey bees	r	P
		Minimum	Maximum	Mean ± SE			
<i>Brassica napus</i>	2023	20.84	31.88	24.46 ± 1.77	0.179 ± 0.045	0.117	0.666
	2024	20.53	30.91	26.24 ± 0.76	1.113 ± 0.085	0.290	0.276
<i>Malus halliana</i>	2023	13.22	27.06	21.65 ± 0.99	0.065 ± 0.023	0.372	0.156
<i>Robinia pseudoacacia</i>	2023	17.00	38.16	28.27 ± 1.56	0.034 ± 0.009	0.222	0.409
<i>Trifolium repens</i>	2023	20.00	34.56	26.91 ± 1.03	0.017 ± 0.003	0.518	0.040
	2024	25.13	31.81	29.23 ± 0.58	0.291 ± 0.060	0.303	0.253
<i>Coreopsis basalis</i>	2023	23.91	39.06	32.98 ± 1.27	0.488 ± 0.053	0.650	0.006
<i>Cuphea hookeriana</i>	2023	22.47	32.88	26.75 ± 0.86	0.229 ± 0.036	0.701	0.002
<i>Zinnia elegans</i>	2023	24.00	41.72	32.28 ± 1.28	0.744 ± 0.101	0.334	0.206
<i>Tagetes erecta</i>	2023	28.03	37.84	32.24 ± 0.64	0.069 ± 0.015	0.066	0.809
<i>Hypericum monogynum</i>	2023	24.28	29.59	26.27 ± 0.32	0.365 ± 0.115	-0.388	0.096
	2024	27.35	38.65	32.52 ± 0.65	0.188 ± 0.018	0.167	0.507
<i>Nandina domestica</i>	2023	23.47	31.97	26.45 ± 0.50	0.400 ± 0.031	0.197	0.448
<i>Viburnum chinshanense</i>	2023	16.09	24.69	19.51 ± 0.29	0.153 ± 0.026	-0.095	0.538
	2024	23.56	36.94	28.83 ± 0.52	0.344 ± 0.049	-0.110	0.511
<i>Aesculus chinensis</i>	2024	31.65	34.35	33.72 ± 0.16	0.135 ± 0.013	0.310	0.225
<i>Viburnum awabuki</i>	2024	30.48	35.85	33.63 ± 0.35	0.456 ± 0.107	-0.238	0.375
<i>Campsis grandiflora</i>	2024	30.10	41.30	35.49 ± 0.74	0.515 ± 0.031	-0.283	0.256

these plant species were visited by several insect species in the field, honey bees (i.e., *A. cerana* or *A. mellifera*) were the primary flower visitors of these species at both sites during our observation. Notably, the flowers of species at Site 1 were visited by the eastern honey bee *A. cerana*, while the western honey bee *A. mellifera* visited the flowers of species at Site 2.

Visitation rate and temperature

To estimate the visitation rates of honey bees, one 50 × 50 cm² patch was randomly selected to observe honey bee activity during the peak bloom of each flowering species. We recorded the number of flowers visited by honey bees in 30-minute sessions between 0700 h and 1800 h on clear days while we counted the total number of observed flowers in the patch to calculate the visitation rate (visits per flower per 30 min). In species of the Asteraceae, where individual florets cannot easily be observed and counted in the field, each capitulum was considered a flower unit. Each plant species was observed for at least 480 minutes (i.e., 16 sessions). A total of 10440 minutes (i.e., 348 sessions) of observations for 14 cultivated plant species were conducted. Moreover, the ambient temperature at flower height was recorded automatically at 15-minute intervals using an electronic temperature recorder (DS1925, Maxim/Dallas Semiconductor Inc., Wilmington, MA, USA). The temperature in each 30 min was obtained by averaging two 15 min temperatures.

Statistical analyses

To assess whether the visitation rate of honey bees was correlated to diurnal temperature, we conducted a Pearson correlation analysis to detect the relationship between the visitation rate and diurnal temperature in each flowering species. The Pearson correlation analysis was performed in SPSS V. 19.0 (SPSS Inc., USA). To examine whether the visitation rate of honey bees responds to the different times of day, we fitted a linear mixed effects model (LMM) to the visitation rate. We used the fixed effect of different times of day (i.e., forenoon, noon, and afternoon) and the random effect of plant species. Data of visitation rate were transformed by square root to achieve normal distribution. We performed a generalized linear model (GLM) with Gaussian distribution and identity-link function to compare the differences in temperatures in the forenoon, noon, and afternoon (with temperature as a dependent variable and different times of day as factors). Linear mixed model and GLM were performed using the software R version 4.0.3 (www.r-project.org).

Linear mixed model and GLM were conducted using the R package of *lmerTest* (Kuznetsova et al., 2017) and *stats*, respectively. The statistical significance of effects was determined with type III Wald χ^2 ANOVA tests in the package *car* (Fox & Weisberg, 2011). Contrasts of estimated marginal means (adjustment method: Tukey) were computed to compare the different time combinations in the analyses (emmeans R package; Lenth, 2020).

Results

Effects of temperature variation on visitation by honey bees

Correlation analyses showed that diurnal temperature variation was significantly positively correlated with the visitation rate of honey bees only in three plant species (i.e., *Trifolium repens*, $r = 0.518$, $p = 0.04$; *Coreopsis basalis*, $r = 0.65$, $p = 0.006$; *Cuphea hookeriana*, $r = 0.701$, $p = 0.002$, respectively; see Table 1). Based on our observations, honey bees began visiting flowers when ambient temperature exceeded 16 °C. Overall, the visitation rate increased almost continuously over the foraging temperature range of 16–42 °C, from 0.119 ± 0.046 visits per flower per 30 min in the range of 14–18 °C up to 0.466 ± 0.06 visits per flower per 30 min in the range of 38–42 °C, except for the range of 34–38 °C, in which a decrease in the visitation rate occurred (Fig 1). The optimal temperature range for foraging honey bees was 38–42 °C (Fig 1). In Fig 2, the relative abundance values were presented for each temperature range and expressed as percentages of the mean visitation rate at its peak (i.e., temperature range with maximum visitation rate; see Herrera, 1990). Moreover, the 75% threshold was chosen to separate high versus low abundance (Herrera, 1990). The abundance of honey bees was high in the temperature ranges 30–34 °C and 38–42 °C (Fig 2).

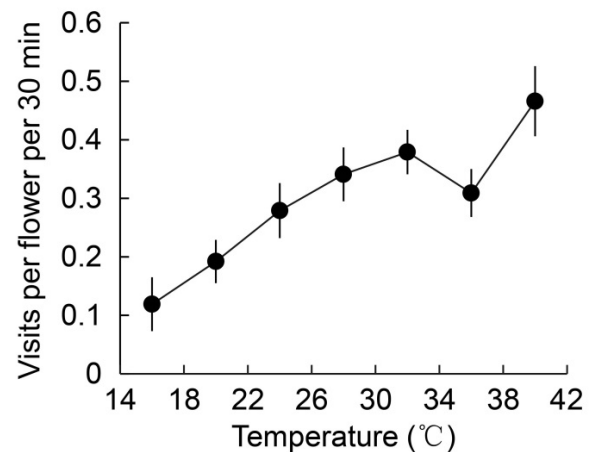


Fig 1. Visitation rate of honey bees at different temperature ranges.

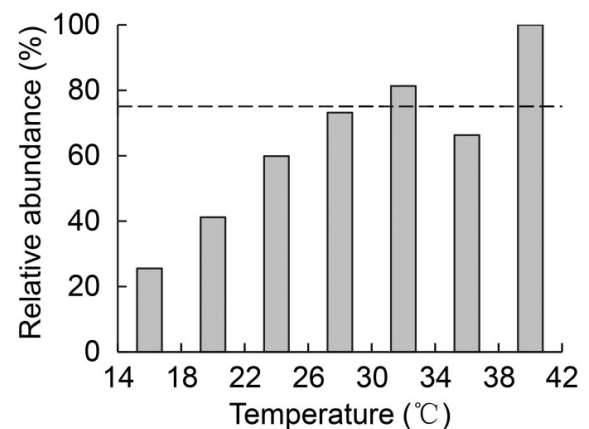


Fig 2. Relative abundance of honey bees at different temperature ranges. The dashed line represents a high abundance (i.e., 75%).

Diurnal variation in visitation rate of honey bees and temperature

Generally, honey bees visited flowers after 0800 h, and the visitation rate increased with ambient temperature until 1100 h (Fig 3). The abundance of honey bees was high from 1000 h to 1700 h (Fig 4), while the visitation rate remained relatively constant without a prominent peak. The visitation rate decreased dramatically after 1700 h. The optimal visitation time for honey bees was 1400-1500 h (Fig 3). The ambient temperature rose with the time of day until 1400 h, with a peak occurring in the period 1300-1400 h, and

then gradually declined (Fig 3). Accordingly, the optimal visitation time did not correspond to the maximum average temperature (32.35 ± 1.08 °C) during the daytime. Both the visitation rate and temperature in the noon and afternoon were significantly higher than that in the forenoon (LMM, Time $\chi^2 = 9.737$, $df = 2$, $p = 0.007$; and GLM, $\chi^2 = 15.076$, $df = 2$, $p < 0.001$, respectively; Fig 5). However, neither the visitation rate nor temperature significantly differed between noon and afternoon (Fig 5). It suggested that honey bees tended to visit more flowers in the noon and afternoon when the temperature was higher.

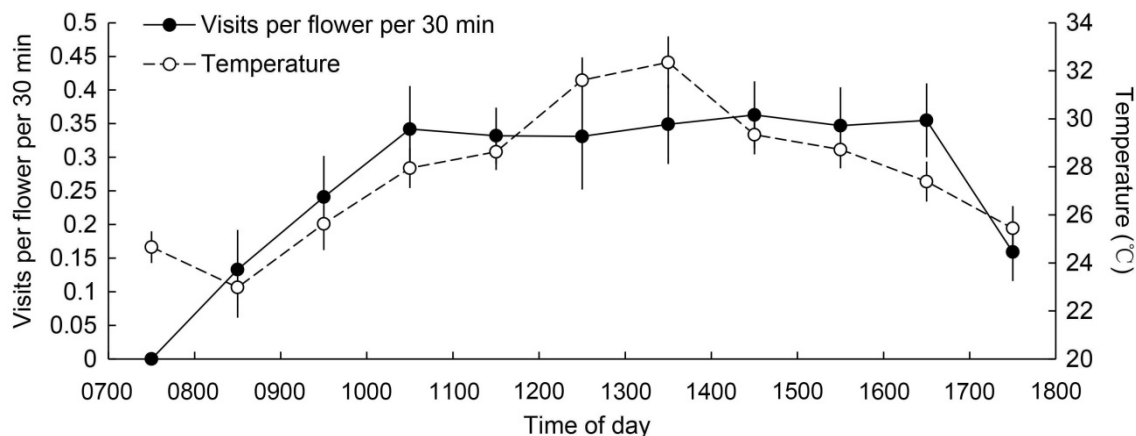


Fig 3. Diurnal variation in visitation rate of honey bees and temperature.

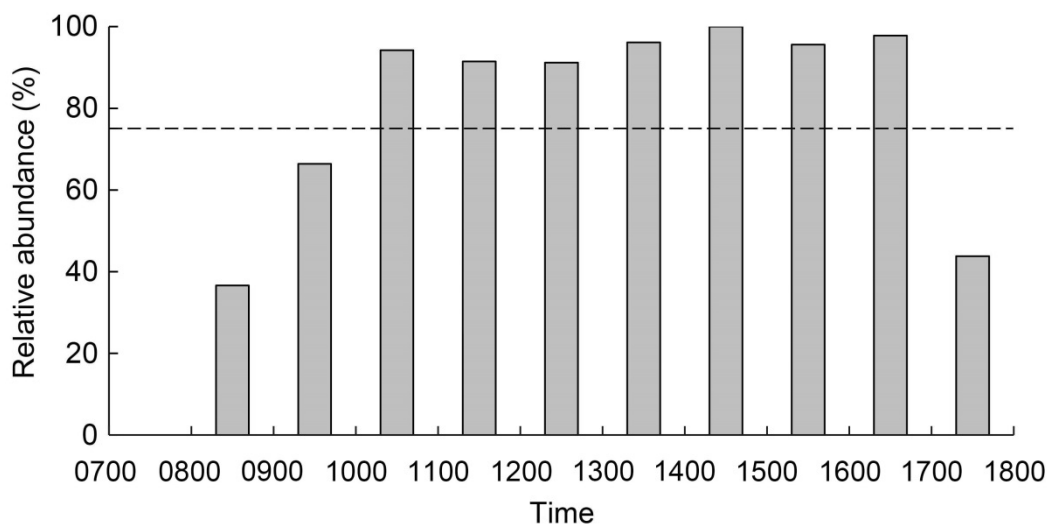


Fig 4. Diurnal variation in the relative abundance of honey bees. The dashed line represents a high abundance (i.e., 75%).

Discussion

Our comparison of the visitation patterns of honey bees (i.e., *A. cerana* and *A. mellifera*) concerning diurnal temperature and time suggested that honey bees tended to visit more flowers in the noon and afternoon when the temperature was higher than in the forenoon. The maximum average

temperature (32.35 ± 1.08 °C) occurred in the period 1300-1400 h, while the optimal visitation time for honey bees was 1400-1500 h, which did not correspond to the maximum average temperature. It suggested that honey bee visitation to flowers was probably affected by the time of day and temperature.

The interaction between thermal balance and diel rhythmicity is responsible for many insect activity patterns

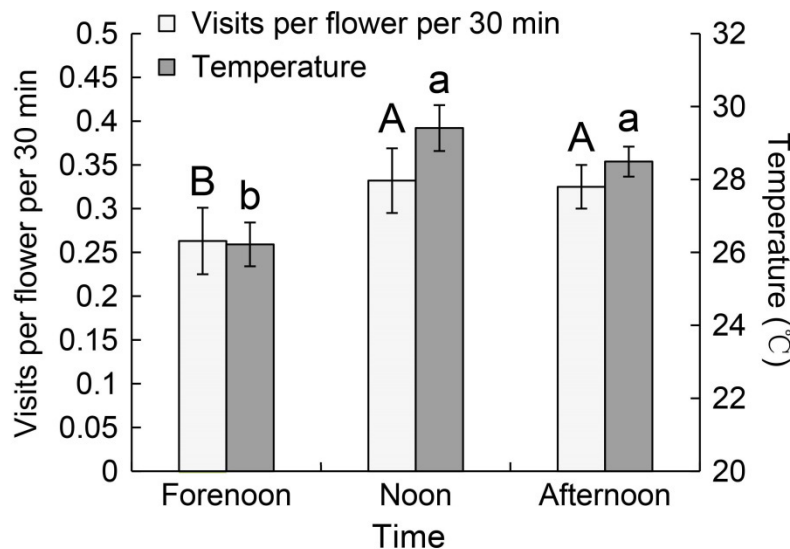


Fig 5. Comparison of visitation rate of honey bees and temperature in the forenoon, noon, and afternoon. Different letters above the bars show significant differences at $P < 0.05$ (GLMs).

(Herrera, 1990). Herrera (1990) investigated the daily activity patterns of the pollinators of a summer-flowering Mediterranean shrub, *Lavandula latifolia*, and showed that honey bees (*A. mellifera*) were most active early in the morning and late in the afternoon since overheating limited their foraging activity at the middle of the day. The ambient temperature range during our observations was 13.22–41.72 °C (Table 1), and the optimal temperature range for foraging honey bees was 38–42 °C. *Apis mellifera* can forage at ambient temperatures up to 46 °C (Herrera, 1990). Therefore, honey bees did not risk overheating at our study sites. Conversely, the low temperature was probably a limiting factor, as we found that honey bees did not visit flowers when the ambient temperature was below 16 °C. Lower temperatures probably resulted in lower visitation rates by reducing the velocity of flight, warm-up rate, and an insect's ability to initiate flight (Arroyo et al., 1985; Corbet et al., 1993). It is thus not surprising that honey bees tended to visit more flowers in the noon and afternoon when the temperature was higher than that in the forenoon at our study sites.

Our results showed that the abundance of honey bees was high from 1000 h to 1700 h, and the visitation rate remained relatively constant without a prominent peak. Moreover, the ambient temperature exhibited an unimodal pattern during the daytime. Therefore, our results did not support the point that comparing insect activity at different temperatures under similar environmental conditions should yield variation in the visitation rates proposed by Arroyo et al. (1985). Particularly, the temperature increased continuously from 27.95 ± 0.83 °C in the period 1000–1100 h up to 32.35 ± 1.08 °C in the period 1300–1400 h, while the visitation rates were 0.342 ± 0.064 visits per flower per 30 min and 0.349 ± 0.059 visits per flower per 30 min, respectively (Fig 3). In addition, our investigation of the effects of temperature variation on visitation by honey

bees partially (3 of 14 species) supported the hypothesis that the visitation rate of honey bees increases with temperature during the daytime (Table 1). It suggested that the visitation rate of honey bees was not affected independently by diurnal temperature variation, and this could explain why the visitation rate increased continuously over the foraging temperature range of 16–42 °C while a decrease occurred in the range of 34–38 °C.

Based on our investigations, honey bees generally started visiting flowers after 0800 h, and they were most active from 1000 h to 1700 h, which is consistent with the findings of previous studies that honey bee *A. mellifera* showed high forage activity between 1000h and 1700 h on flowers of *Phacelia tanacetifolia* for nectar collection (Thrasylvoulou & Basilis, 1998; Owayss et al., 2020). However, Nishanthini and Kanagarajan (2024) found that the peak activity of honey bees (*Apis cerana indica* F.) occurred in the period 0600–1000 h at different migratory sites in Southern India, and they made about 90% of their flower visits in the early morning, even if plenty of flowers were available throughout the day. This pattern is because all of the migratory sites in Southern India are located in southernmost latitudes, where solar radiation intensity is higher than in northernmost latitudes. Honey bees decreased their activity with rising solar radiation intensity at the migratory sites (Nishanthini & Kanagarajan, 2024). In this case, honey bees focused their activity early in the morning to avoid solar radiation. In our study, both sites are located in middle latitudes, and the foraging activity of honey bees may not be significantly affected by solar radiation as they were most active in the noon and afternoon.

Additionally, honey bees fixed their daily foraging patterns depending on their foraging time sense that they obeyed a diurnal pattern of activity driven by factors such as memory or the time of reward availability (Bennett & Renner, 1963; Moore

& Rankin, 1983; Lehmann et al., 2011). Honey bees avoid the time that can hinder their foraging or even be dangerous (Nishanthini & Kanagarajan, 2024), while they can precisely associate the time of day with the presentation of a food reward (Moore & Rankin, 1983). It suggested that the time of day was also a crucial factor in determining the visitation pattern of honey bees.

Honey bees are valued not only for honey production but also as effective pollinators of many wild plants and crops. In order to adapt to various geographical environments, honey bees exhibited different daily foraging patterns depending on various factors (Herrera, 1990; Young et al., 2021; Nishanthini & Kanagarajan, 2024). In this study, we focused on the effects of diurnal temperature and time on honey bee visitation to flowers. Our results suggested that honey bees tended to visit more flowers in the noon and afternoon when the temperature was higher than in the forenoon. This study enhances our understanding of the visitation patterns of honey bees concerning diurnal temperature and time and provides a valid theoretical basis for protecting and caring for honey bees.

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Authors' Contributions

LDF: conceptualization, resources, methodology, investigation, writing-original draft, writing-review & editing, project administration, funding acquisition.

TJ: conceptualization, resources, methodology, investigation, writing-original draft, writing-review & editing, project administration, funding acquisition.

FXD: methodology, investigation.

CYD: methodology, investigation.

LZ: methodology, investigation.

LAT: methodology, investigation.

HYT: methodology, investigation.

YXC: conceptualization, methodology, resources, writing-review & editing.

Data availability

The raw data of the study are uploaded as supplementary material.

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