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Foraging behavior and work patterns of *Bombus terrestris* (Hymenoptera: Apidae) in response to tomato greenhouse microclimate

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Bumblebees play a significant role as pollinators for many wild plants and cultivated crops, owing to their elongated proboscis, resilience to diverse weather conditions, robustly furred bodies, and their unique capacity for buzz-pollination. To better understand the effect of greenhouse microclimates on bumblebee foraging behavior and working modes, a long-term record of foraging activity for each *Bombus terrestris* L. (Hymenoptera: Apidae) forager was monitored by the Radio-frequency identification system. The pattern of task performance, including constant housing, foraging, and day-off rotation, was examined under the microclimate. In addition, the correlation between foraging activity of bumblebees and temperature, relative humidity, illumination in the greenhouse, and pollen viability of tomato plants was further analyzed. Our findings revealed that *B. terrestris* can respond to microclimatic factors and plant resources while also exhibiting a suitable working pattern within the colony. Day-off rotation was observed as a strategy employed by foragers to prolong their survival time. This division of labor and task rotation may serve as strategies for the survival and development of the colony. Our research may contribute to fully understanding how microclimate and plants influence pollinator behavior within greenhouses, thereby optimizing the pollination management of bumblebees on greenhouse crops.

Key words: foraging behavior, division of labor, day-off rotation, environmental factors, pollen viability

Introduction

Bees are essential for plant pollination in both natural and agricultural ecosystems (Stanley et al. 2017, Nayak et al. 2020, Lyu et al. 2023). They have developed remarkable adaptability and are able to interact harmoniously with plants and their surrounding environment as a result of pollinator-plant co-evolution (Wahengbam et al. 2019). Specifically, bumblebees work well in the enclosures and approximately 95% of commercially-reared bumblebee colonies are being used in the production of various greenhouse crops worldwide, particularly tomatoes (Velthuis and Van Doorn 2006, Zameer et al. 2022). The buff-tailed bumblebee, *Bombus terrestris* L., is the predominant species commercially-reared for over three decades (Rasmont et al. 2008). In addition to the aforementioned characteristics, *B. terrestris* exhibit cooperative foraging and division of labor, which further enhances their effectiveness as pollinators (Beshers and Fewell 2001, Holbrook et al. 2011, Johnson and Frost 2012). Division of labor among workers (polyethism) is the key adaptation of eusocial insects that has promoted their ecological success (Wilson 1990, Biedermann and Taborsky 2011). In mature bumblebee colonies, certain individuals exhibit specialization in particular tasks (Cartar 1992, Hagbery and Nieh 2012, Ge et al. 2023). This specialization is deemed adaptive for social groups as it enhances collective efficiency. Nevertheless, colonies often achieve optimal performance when they comprise both specialized and flexible individuals (Oster and Wilson 1978, Muller and Chittka 2008, Fisher et al. 2019). Bumblebee workers can also engage in multiple tasks, sometimes within a single day (Jandt et al. 2009, Crall et al. 2018), as the individuals have the capacity to adapt their behavior in response to the current needs of the colony (Free 1955, Fisher et al. 2022).

Social bees establish a vital connection between the internal environment and external environment of the nest through their foraging behavior (Dunlap et al. 2017, Incorvaia et al. 2021). Therefore, both internal and external factors, including the management of brood and pollen storage within the colony (Forrest 2017, Gerard et al. 2023), the availability of flowering plants (Kitaoka and Nieh 2009, Zhang et al. 2019), and the climate in the surrounding environment (Kenna et al. 2021, Maebe et al. 2021, Karbassioon et al. 2023) may impact their foraging activity and pollinating effectiveness. Pollinators and flowering plants have developed remarkably adaptive strategies as a result of sharing a long history of co-evolution (Kearns et al. 1998, Pyke 2016). Bees have evolved specialized sensory systems to assess the value of distinct flowers and make the profitably foraging decisions, which is essential for the survival and reproductive success of both pollinators and flowering plants (Krishna and Keasar 2018). When floral resources are inadequate, bees exhibit a low frequency of foraging trips (Polatto et al. 2014). Pollen availability is likely a critical determinant influencing a bee's choice of flowers to visit (Brunet et al. 2015, Harmon-Threatt et al. 2017). It was documented that bumblebees can pinpoint the unvisited flowers by recognizing the quantity of available pollen during their flight over the open flowers (Zimmerman 1982, Harder 1990). They differentiate the recently visited from unvisited flowers to avoid revisiting flowers and to access superior pollen resources for their colony.

In addition to floral resources, climate factors such as temperature, light intensity, humidity, and wind speed influence the foraging behavior of bees, both in open fields and greenhouses (Corbet et al. 1993, Vicens and Bosch 2000, Karbassioon et al. 2023). Bees have been observed to increase their foraging behaviors before storms or rainy days, which may be part of their behavioral strategies to cope with weather changes and increase population survival (He et al. 2016b). Moreover, ambient temperature and light intensity can affect the foraging flight of bees by altering their body temperature (Polatto et al. 2014). Bees respond to a wide range of environmental conditions and adapt their foraging behavior accordingly, owing to their capacity for thermoregulation (Heinrich and Esch 1994, Kovac et al. 2019). Since changes in temperature and precipitation significantly influence the physiology and phenology of flowering plants, weather conditions can also impact bees' foraging behavior by altering the quality and quantity of their food resources (Corbet 1990, Gray and Brady 2016). Consequently, the sensory ecology and neurobiology underlying the interaction between bees and their environment, particularly concerning climate dynamics, present a promising, and valuable avenue for research.

Radio-frequency identification (RFID) technology, which utilizes radio waves to automatically read special tags affixed to the thoraxes of individual bees, is a convenient method for monitoring the behavior of social bees as the tagged individuals pass through a scanner (Nunes-Silva et al. 2019). This technology enables continuous automatic monitoring of a large number of bees, and it has proven to be highly valuable in assessing the bee's foraging behavior, navigation, and survival (Henry et al. 2012, He et al. 2013, Russell et al. 2017). Moreover, it has the potential to track individual bees over their lifetimes, providing insights into how the group's work patterns and division of labor adapt to environmental changes. With the rapid expansion of greenhouse tomato cultivation in northern China (He et al. 2016a, Yang et al. 2022), it is crucial to thoroughly investigate the foraging behavior and work patterns of the most commonly used commercial bumblebee pollinator (*B. terrestris*) for tomatoes within the microclimate of greenhouses. In this study, we utilized RFID technology to compile a comprehensive lifetime record of foraging activity for each tagged *B. terrestris* forager and addressed three key questions. (i) What are the work patterns of bumblebee foragers? (ii) How does microclimate affect the foraging activities and work patterns of bumblebee foragers in greenhouses? (iii) What's the relationship between the flower visiting behavior of bumblebee foragers and pollen viability? Our findings would provide fully understand of pollinator activity and working patterns in microclimate of greenhouse and improve service efficiency of bumblebees on tomato plants.

Materials and Methods

Bumblebees

Three bumblebee colonies of *B. terrestris* containing 1 queen and 160 worker bees were used in the experiment. They were provided by Institute of Plant Protection, Beijing Academy of Agricultural and Forestry Sciences, and maintained in dark conditions at a temperature of 27 ± 1°C and a relative humidity of 55 ± 5%. The colonies were established by sister queens to ensure uniform genetic backgrounds and were kept in cages measuring 30 × 30 × 21 cm (L × W × H). All manipulations were conducted under red light to minimize disturbance. Syrup and pollens were supplied to the colonies until they reached an appropriate size (more than 120 workers per colony) for solar greenhouse pollination located in Beijing, China. At that point, pollen was removed to encourage worker bees to forage in the solar greenhouse. In each greenhouse compartment, covering an area of 600 m², 2,500 tomato seedlings were planted, and pollinated by one colony of bumblebees. The cultivation in these compartments followed a consistent protocol for both management and agricultural operations. Real-time weather data, including light intensity, relative humidity, temperature in greenhouse were recorded using a meteorological sensor (UbiBot GS1 AL4G1RS 4G + WiFi).

RFID System

The RIFD system was developed and manufactured by the Honeybee Research Institute of Jiangxi Agricultural University in collaboration with the Guangzhou Invengo Information Technology Co., Ltd (He et al. 2013). The system used in our study contained five main components: tags, two antennas, a reader, a wireless router, and a data storage platform. Tags, circular disks with a diameter of 3 mm, thickness of 0.05 mm, and weight of 1 mg, were glued to the thoraces of bumblebees using a shellac-based adhesive following CO_2-induced anesthesia. An ultrahigh-frequency (UHF) signal (920–925 MHz) was emitted by the tag, which had a unique digital ID composed with 6 numbers or letters. Two antennae were placed in a tunnel that was connected to the hive entrance. The tagged bees can be scanned as they pass through the hive tunnel, with their passage time and digital number recorded by a reader simultaneously. Bees passed through antenna 1 before antenna 2 upon entering the colony, and the sequence was reversed upon exiting the colony. Flight duration was considered a foraging trip when it lasted more than 1 min.

Working Pattern and Foraging Behavior of Bumblebee Workers

All the workers from the three colonies were tagged and their entering and exiting behaviors from the nest were continuously monitored for 26 days by RFID system. 'Constant house bees' referred to individuals within the colony that have been never monitored leaving the colony, while 'outgoing bees' were those that exited the nest at least once (Free 1955). 'Constant foragers' were defined when 'outgoing bees' engaged in foraging for at least 3 days. Constant foragers were categorized into two groups: rotating day-off bees, which had rotated for more than one day-off during the foraging period, and nonrotating bees, which never took a day-off during the foraging period (Shi et al. 2020). The working time of foragers was defined as the number of days on which workers engaged in foraging trips. In this study, the survival time of the foragers was defined as the period from the start of the experiment until the last time they were scanned by RFID.

Viability of Pollen

Pollen viability was assessed at different time points (9:00, 10:30, 12:00, 13:30, 15:00, 16:30) using the TTC (2, 3, and 5-triphenyl tetrazolium chloride) test (Huang et al. 2004). At each time point, four flowers were collected to examine the pollen viability when the fresh flowers were fully opened (Amala and Shivalingaswamy 2017). These flowers were individually isolated in the morning at the prebloom stage to prevent any potential influence from visitors on pollen viability. Freshly harvested anthers were immersed in 200 μL of 1% TTC solution (pH = 7.4) and gently stirred to ensure the even dispersion of pollen grains within the TTC solution. Ten μL of TTC solution containing pollen grains was added onto a microscope slide, which was then immediately covered with a coverslip. After the 30 min incubation at 35°C, the slides were placed under a stereomicroscope (SZX 16, Olympus, Tokyo, Japan) for the observation and calculation of pollen viability. Viable pollen grains exhibited a staining reaction ranging from dark to light pink, while no color reaction occurred for dead pollen grains. The viability of pollen was calculated by dividing the number of viable pollen grains by the total number of pollen grains.

Flower Visiting Behavior of Bumblebee Foragers

The flower visiting behavior of bumblebee foragers was observed directly and documented from 9:00 to 17:00. The number of flowers visited by a single foraging bee per minute was defined as the flower visitation rate. The monitoring weas conducted every 30 min, with 10 individual bee visitors observed each time. During the same period, the time spent by bees foraging on each flower was investigated as well. Ten flowers were monitored for each time interval.

Data Analysis

All the statistical analyses were performed using SPSS 25.0 software (SPSS Inc, Chicago, USA). The *t*-test was used to compare the difference in percentages between constant house bees and outgoing bees, the difference in percentages of outgoing bees between periods exceeding 3 days and those less than 2 days, and the difference in percentages of constant foragers between rotation and off rotation. Additionally, the differences in total foraging frequency, daily foraging frequency, survival time, and working time between the day-off rotating bees and nonrotating bees were also analyzed by the *t*-test. The impact of cloudy weather (day 13) on the number of foragers and their total foraging frequency in all foraging individuals, rotating day-off and nonrotating foragers was analyzed with univariate analysis in a linear model, followed by a Tukey's HSD test for multiple comparisons among days 12 to 14.

To assess the relationship among the foraging activities, abiotic, and biotic factors in tomato greenhouse, both correlation (r) and linear regression (R^2) analyses were conducted. Correlation between the number of foragers, total foraging frequency, pollen viability, the flower visitation rate, and either temperature or illumination was tested using a Pearson method (PC: Pearson correlation). Additionally, correlation between the flower visitation rate of foragers and the pollen viability of tomato flowers was also analyzed by the Pearson method. Correlation between the number of foragers, total foraging frequency, pollen viability, and relative humidity, as well as correlation between the time spent by bees on each flower, and their working time, were examined using the Spearman method (SC: Spearman correlation). The relationship between foraging activities and three environmental factors were analyzed in linear mixed models, with colony and day considered as random factors. Moreover, other relationships, including those between pollen viability and environmental factors, flower visiting rate and pollen viability, and time spent of forager on each flower and their working time, were examined using simple linear regression (SLR). All figures were generated using GraphPad Prism 9.

Results

Working Pattern of Bumblebees in Greenhouse

As shown in Fig. 1, in the bumblebee colony, outgoing bees accounted for approximately 63.74%, significantly higher than the proportion

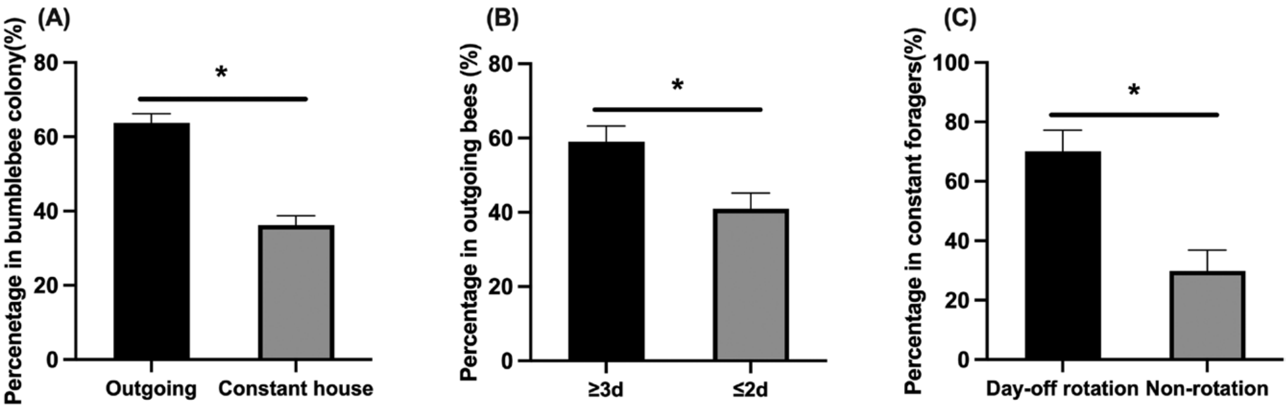

Fig. 1. Tentatively working pattern in *B. terrestris* colony. A) the percentage of outgoing bees in bumblebee colony; B) the percentage of constant foragers in outgoing bees; C) the percentage of the rotating day-off bees in constant foragers. * indicates a significant difference at $P < 0.05$.

of constant housing individuals ($t = 7.754$, $df = 4$, $P = 0.001$, Fig. 1A). Approximately 59.03% of all outgoing bees were constant foragers; the proportion was significantly higher than that of bees foraging for less than 2 days ($t = 3.027$, $df = 4$, $P = 0.039$, Fig. 1B). Among the constant foragers, rotating day-off bees accounted for a significantly larger proportion, approximately 70.14%, compared to nonrotating foragers ($t = 4.406$, $df = 4$, $P = 0.016$, Fig. 1C). There was no significant difference in the total foraging frequency per bee between day-off rotation and nonrotation ($t = 1.467$, $df = 177$, $P = 0.144$), while the daily foraging frequency of nonrotating bees was significantly higher than that of rotating day-off bees ($t = 4.496$, $df = 177$, $P < 0.001$, Fig. 2A). Moreover, there was no significant difference in working time between rotating day-off and nonrotating foragers ($t = 1.769$, $df = 177$, $P = 0.079$). Nevertheless, the survival time of nonrotating foragers was significantly shorter than that of rotating day-off bees ($t = 5.365$, $df = 177$, $P < 0.001$, Figs. 2B and 3).

Foraging Behavior of Bumblebees in Greenhouse

Throughout the entire monitoring period, no correlation was observed between the number of foragers, total foraging frequency, and environmental factors, i.e., temperature, relative humidity, and illumination (Supplementary Fig. S1 and Table S1). However, The number of foragers and their total foraging frequency were positively correlated with the mean daytime temperature and negatively correlated with the mean daytime humidity in the greenhouse during day 1–15 (Supplementary Fig. S2 and Table S1). In addition, on the cloudy day (day 13), both the number of all foragers ($F_{2,6} = 13.168$, $P = 0.006$, Fig. 4A) and their total foraging frequency ($F_{2,6} = 9.137$, $P = 0.015$, Fig. 4B) were significantly lower compared to the first sunny day (day 14) following the cloudy day. Cloudy weather had the same influence on the number of rotating day-off foragers ($F_{2,6} = 43.969$, $P < 0.001$, Fig. 4A) and their foraging frequency ($F_{2,6} = 11.772$, $P = 0.008$, Fig. 4B) as it did on all foraging individuals. However, no significant difference was found in the number of nonrotating foragers ($F_{2,6} = 0.139$, $P = 0.873$, Fig. 4A) and their foraging frequency ($F_{2,6} = 0.992$, $P = 0.424$, Fig. 4B) between different weather conditions. The daily foraging behavior of bumblebees was analyzed over three consecutive days (Days 3–5) in the greenhouse, showing a strong association with environmental factors, including temperature, relative humidity, and illumination. Both the number of foragers (temperature: $r = 0.878$, $P < 0.001$, illumination: $r = 0.678$, $P < 0.001$, PC) and their total foraging frequency (temperature: $r = 0.857$, $P < 0.001$, illumination: $r = 0.651$, $P < 0.001$, PC) were positively correlated with the temperature and luminous intensity, but they were negatively correlated with the relative humidity (the number of foragers: $r = -0.812$, $P < 0.001$, total foraging frequency: $r = -0.867$, $P < 0.001$, SC) in the greenhouse. Moreover, as depicted in Fig. 5, the correlation between the number of bumblebee foragers and their total foraging frequency can be modeled through linear equations based on temperature (Fig. 5A and D), relative humidity (Fig. 5B and E), or illumination (Fig. 5C and F).

Pollen Viability of Tomato and Flower Visitation Rate of Foragers

The pollen viability of tomato flowers was positively correlated with the real-time temperature (PC: $r = 0.837$, $P < 0.001$), and light intensity (PC: $r = 0.901$, $P < 0.001$) in the greenhouse, but it was negatively correlated with relative humidity (SC: $r = -0.484$, $P = 0.042$) in the greenhouse. Moreover, the pollen viability was well-fitted to a linear equation based on temperature or illumination rather than humidity, as shown in Fig. 6. A significantly linear positive correlation was observed between the floral visitation rate of bumblebee foragers and pollen viability (PC: $r = 0.953$, $P = 0.003$, Fig. 7A). However, the time spent by the foragers on each tomato flower was positively correlated with their working time in the greenhouse (SC: $r = -0.721$, $P < 0.001$, Fig. 7B).

Discussion

Bumblebees are not only economically important pollinators but also serve as a primary model system for various studies in social behavior and ecology (Goulson 2010). In the present study, the RFID system was used to monitor all the tagged bumblebee individuals throughout their survival time. Task performance and foraging activity were investigated within the tomato greenhouse of commercial bumblebee colonies. The *B. terrestris* colony allocated a fixed proportion of worker individuals for working outside the nest, and established a work pattern of day-off rotation to extend the survival time of foragers. In addition, individual foragers can adjust their workload and visitation rate on tomato flowers according to the dynamic variation in microclimate and pollen viability within the greenhouse.

Social insects, including bumblebees, exhibit a clear division of labor and cooperation within their colony. In our study, we observed that approximately one third of the worker individuals were 'constant house bees', remaining within the nest even in the absence of artificial pollen. These individuals may be considered professionally housing bees, specializing in tasks within the nest, such as caring for larvae, and cleaning the nest (Chittka and Muller 2009, Jandt et al. 2009). Such behavioral specialization may be genetically predetermined or size-dependent (Ge et al. 2023), as observed in *Bombus griseocollis*

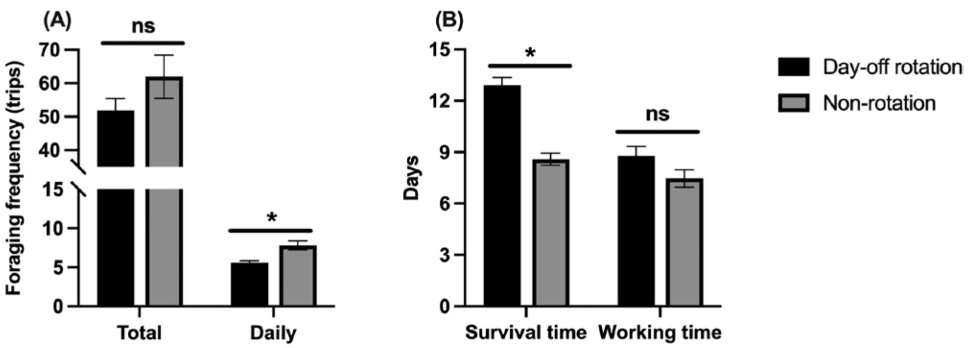

Fig. 2. The total and daily foraging frequency A), survival time and the working time B) between rotating day-off and nonrotating *B. terrestris* foragers. * indicates a significant difference at $P < 0.05$; ns indicates no significant difference.

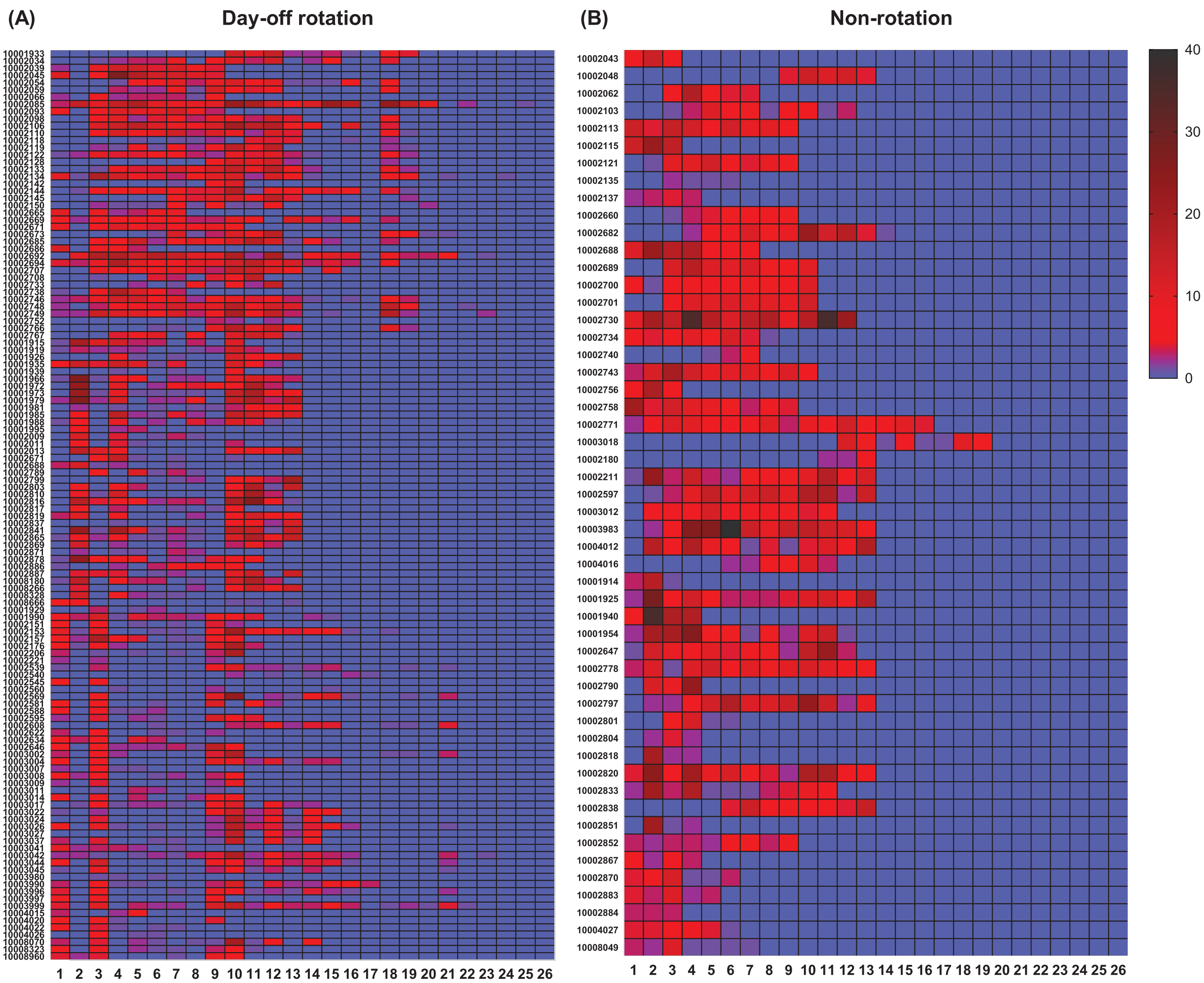

Fig. 3. Heatmap of the foraging trips of rotating day-off and nonrotating foragers across different days.

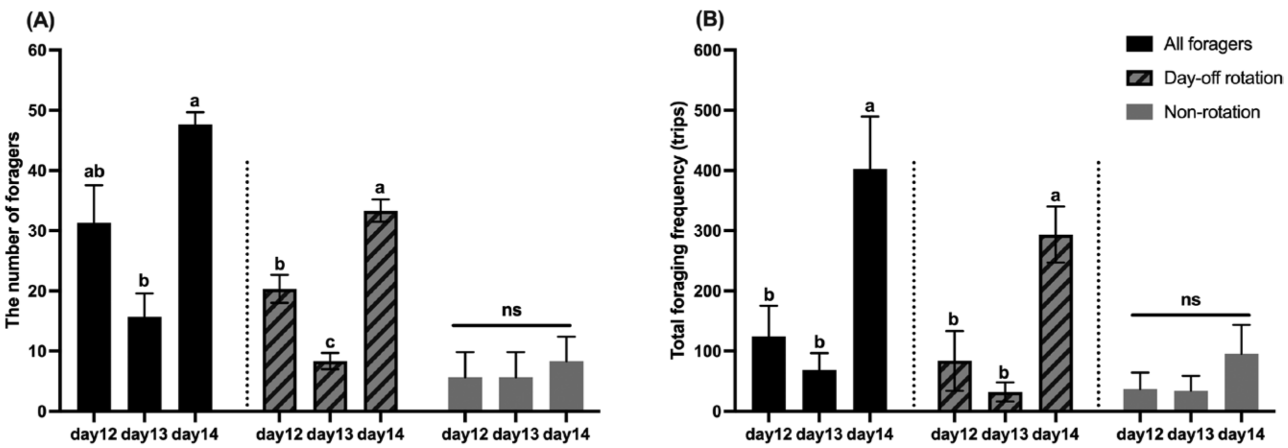

Fig. 4. The number of foraging individuals A) and their foraging frequency B) among all foragers, rotating day-off foragers and nonrotating foragers of *B. terrestris*. Different letters indicate significant differences at $P < 0.05$; ns indicates no significant difference.

workers where the task switching is not rigidly age-dependent (Cameron 1989). Some individuals may never undertake foraging, while others may never engage in guarding duties. Additionally, the percentage of 'constant house bees' within the colony is significantly smaller than that of outgoing bees. This may be correlated to the higher risks associated with working outside the nest (Jandt and Dornhaus 2009). Indeed, within the outgoing bees, there is also a division of tasks. We observed the presence of fake-foragers, which

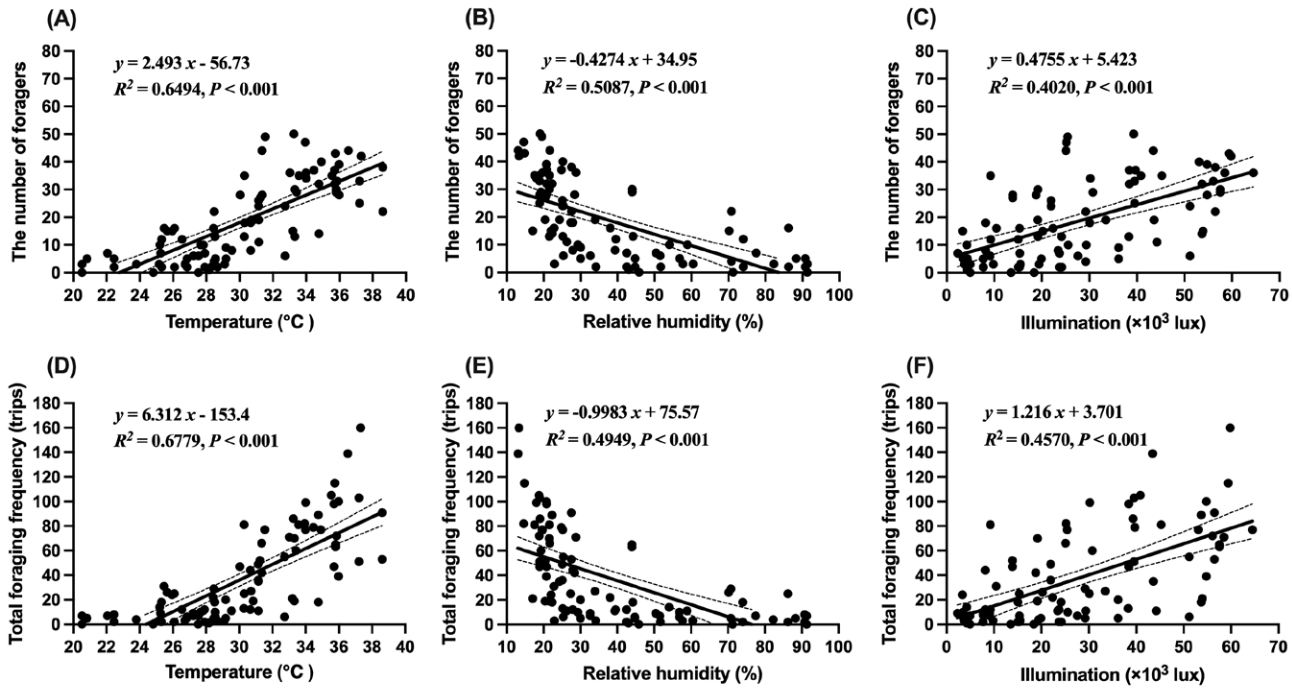

Fig. 5. Relationship between the number of foragers, total foraging frequency of *B. terrestris* in one day and the environmental factors including temperature A and D), relative humidity B and E) and illumination C and F) in the greenhouse.

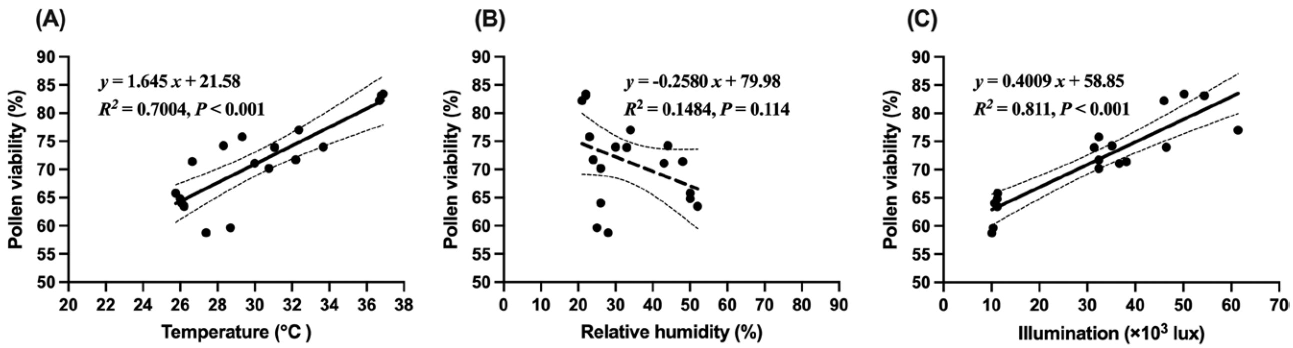

Fig. 6. Relationship between the pollen viability of tomato flowers and the environmental factors, including temperature A), relative humidity B) and illumination C) in the greenhouse.

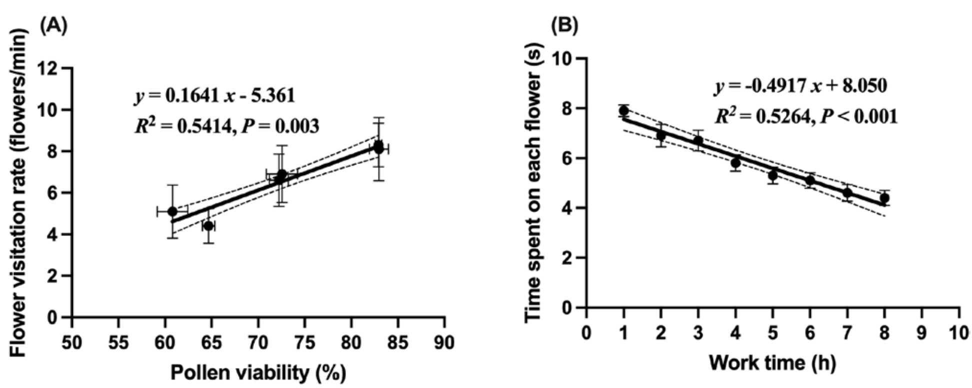

Fig. 7. Relationship between the floral visitation rate of *B. terrestris* foragers on tomato flowers and the pollen viability A); relationship between the time spent on each tomato flower of *B. terrestris* foragers and their work time in one day B).

constituted 2/5 of the outgoing bees and typically only ventured out for 1–2 days. These individuals may serve as explorers responsible for scouting food sources. Our findings underscored a broad distribution of task specialization among bumblebee workers.

While some individuals specialized in a single task, the majority exhibited flexibility by performing multiple tasks (Fisher et al. 2022). As demonstrated in our study, not all constant foragers were engaged in pollination activities throughout the monitoring period. The constant foragers can be categorized into two groups: rotating day-off bees and nonrotating bees. The number of rotating day-off bees is 2.3 times greater than that of nonrotating bees. The bees of day-off rotation may have the ability to switch between household and foraging duties based on the colony's needs (Free 1955). Day-off rotation serves not only as a method for task switching but also as a strategic approach for group development (Tian et al. 2014). Our results indicated that while the daily workload of rotating day-off bees may be lower, their total foraging frequency was not significantly different compared to nonrotating bees. Moreover, the day-off rotation significantly extended the survival time or lifespan of foragers under the same workload. This phenomenon was observed in both bumblebees and honey bees (Tian et al. 2014). Furthermore, the proportion of rotating day-off bees in honeybee foragers increased when they were exposed to sublethal doses of insecticides (Shi et al. 2020, 2024). Consequently, the rotation system observed in social bees may aim to mitigate work intensity and foraging risks while maintaining the foraging efficiency of individuals. Foraging, recognized as a high-risk and energy-demanding task for individual bees, can benefit from the regulated distribution of rest time, minimizing metabolism and limiting energy consumption, thus improving the overall work efficiency of colonies (Stabentheiner et al. 2003, Klein 2018). Therefore, this work pattern may not only improve work distribution and efficiency, but it can also contribute to the overall development and productivity of bee colonies, potentially representing a behavioral strategy evolved by social bees over time.

Weather condition is one of the key factors affected the foraging behavior. As demonstrated in our results, cloudy weather, characterized by the lowest temperature, light intensity, and highest relative humidity, can significantly diminish the foraging activities of bumblebees compared to the subsequent later sunny days. The dramatically enhanced foraging behavior may serve as a compensatory response to offset any foraging deficits experienced by the bumblebees on previously adverse days (Reeves et al. 2023). Moreover, the relationship between the daily foraging behavior of bumblebees and climatic factors as well as pollen resources, demonstrated that temperature and light intensity are more critical weather conditions impacting their foraging frequency, compared to relative humidity in the tomato greenhouse. Similar results were obtained on other bees, such as *Apis mellifera* and *Centris varia* (Polatto et al. 2014). Although the foraging behavior of *B. terrestris* was significantly correlated with all three environmental factors in the tomato greenhouse, temperature was the best-fitting variable under the linear mixed model (Fig. 5). Additionally, pollen viability, a crucial biological signal for attracting bumblebees to forage on tomato flowers, showed stronger correlations with temperature, and illumination rather than humidity in the greenhouse (Fig. 6). This could result from the important impact of temperature and light on bumblebee foraging flights by thermoregulation (Polatto et al. 2014, Glass et al. 2024). Also, light plays a crucial role in the visual navigation of bees, assisting them in orientation as well as search for floral resources (Hilário et al. 2000, Lotto and Chittka 2005). Conversely, the relative humidity is a dependent abiotic factor, contingent upon temperature and solar radiation within the greenhouse. Hence, forager bees respond to the changeable environment by regulating the energy balance between intake and consumption (Stabentheiner and Kovac 2016).

Pollinators possess the ability to detect plants offering the highest food rewards, and plants can emit signals to attract their most efficient pollinators (Sanderson et al. 2015). It is consistent with our findings that the flower visitation rate of bumblebee foragers significantly increases with higher pollen viability, reaching their peak concurrently (Fig. 7A, Supplementary Fig. S3). Besides, both foraging activities and pollen viability are correlated with the microclimate (such as temperature and light intensity), which may contribute to their similar dynamics in the greenhouse. In addition, the forager individuals exhibit a progressive increase in work efficiency over the day, which is likely due to their advanced learning and memory skills of foragers while engaging in foraging tasks (Kamil and Roitblat 1985, Pull et al. 2022). Furthermore, the reduced pollen viability in the late afternoon may prompt bumblebees to accelerate the abandonment of tomato flowers. Overall, bumblebees could detect variations in pollen availability among individual flowers based on environmental cues and adapt their foraging behavior accordingly, prioritizing flowers that offer higher pollen quality and quantity to maximize their foraging rewards.

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Author contributions

Huan Wang (Conceptualization [lead], Data curation [lead], Formal analysis [equal], Funding acquisition [lead], Investigation [equal], Methodology [lead], Visualization [equal], Writing—original draft [lead], Writing—review & editing [equal]), Yanyan Qu (Conceptualization [equal], Data curation [equal], Formal analysis [lead], Funding acquisition [equal], Investigation [supporting], Methodology [equal], Software [lead], Visualization [lead], Writing—original draft [equal], Writing—review & editing [lead]), Xu Jiang He (Formal analysis [equal], Methodology [equal], Software [equal], Writing—review & editing [equal]), Xi-lian Xu (Conceptualization [supporting], Project administration [lead], Resources [equal]), Rufang Wang (Visualization [supporting], Writing—review & editing [supporting]), Meijing Xue (Data curation [supporting], Investigation [equal]), and Zhi-Jiang Zeng (Conceptualization [lead], Resources [equal], Supervision [lead], Writing—original draft [supporting], Writing—review & editing [equal])

Supplementary data

Supplementary data are available at *Journal of Economic Entomology* online.

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