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RESEARCH ARTICLE - BEES

Attractiveness of *Tetragonula laeviceps* (Hymenoptera: Apidae) to Citrus Volatile Compounds and Flower Colors in Indoor Microclimate Conditions

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Abstract

Tetragonula laeviceps plays a vital role as a primary pollinator of citrus flowers for successful pollination. However, there is still a lack of understanding about how *T. laeviceps* can find citrus flowers. This study aimed to elucidate the factors influencing the attraction of *T. laeviceps* to citrus flowers, focusing on microclimate conditions, and visual and olfactory factors. For this, we conducted six-choice assays in a stingless bee house using artificial flowers as visual cues and citrus essential oils as olfactory stimuli. Three pairs of red or white artificial flowers were displayed to adult workers, with each pair placed in glass vials filled with diluted orange (*Citrus reticulata*) essential oil, lemon (*Citrus limon*) essential oil, or solvent. Simultaneously, microclimate conditions were measured, including temperature, relative humidity, and light intensity. We observed that the highest number of *T. laeviceps* visited the artificial flowers at 11:00, irrespective of visual and olfactory factors. We also found a positive correlation between the number of visits and both temperature and light intensity, whereas there was a negative correlation with humidity. The number of visits did not exhibit a significant difference between flower colors. In contrast, we observed the highest visitation to the orange essential oil, followed by the lemon essential oil and solvent. Gas Chromatograph – Mass Spectrometry (GC-MS) analysis revealed common terpenes in orange and lemon essential oils, while linalool and α-citral were predominantly detected in the orange essential oil. These characteristic terpenes could potentially be the attractants for *T. laeviceps*.

Introduction

Orchard farming, such as citrus fruits, still requires insect pollinators to enhance successful fruit production (Aizen et al., 2019; Garibaldi et al., 2011; Grajales-Conesa et al., 2013). However, numerous studies have reported the decline of wild pollinators in various regions (Koh et al., 2016; MacInnis et al., 2023; Panziera et al., 2022; Potts et al., 2010; Rhodes, 2018), resulting in an increased dependence on cultivated bee colonies in agroecosystems (Garibaldi et al., 2011; Hall et al., 2020; MacInnis et al., 2023; van Engelsdorp et al., 2008). Among these managed pollinators, stingless bees could be alternative pollinators in tropical countries (Azmi et al., 2019; dos Santos et al., 2009; Hall et al., 2020; Putra et al., 2014; Roselino et al., 2009). *Tetragonula laeviceps* is one type of stingless bee that is widely cultivated in Indonesia (Buchori et al., 2022) and has become the primary pollinator in citrus orchards, substantially enhancing pollination success (Nurdiansyah et al., 2023).

Plant-pollinator interactions, such as those between citrus flowers and *T. laeviceps*, are facilitated by volatile compounds released from citrus flowers. The volatiles allow *T. laeviceps* to locate the flowers, resulting in mutually beneficial interaction (Beck et al., 2017). Flowers employ various visual

cues to communicate with potential pollinators, including petal color, shape, flower size, and corolla shape, alongside volatile compounds (Raguso, 2008). These signals can act independently or synergistically to enhance the attractiveness of flowers to pollinators (Zhang et al., 2023). Furthermore, microclimate conditions, including temperature, relative humidity, and light intensity, are crucial factors influencing the foraging activity of pollinators in their search for pollen, nectar, and resin (Aizen et al., 2019; Garibaldi et al., 2011; Polatto et al., 2014). In *T. laeviceps*, ambient microclimate conditions also significantly influence the foraging behavior. (Cholis et al., 2020; Garibaldi et al., 2011; Polatto et al., 2014).

Among the various factors, exploring the specific volatile compounds that attract *T. laeviceps* is of particular interest because these compounds serve as the initial cues for *T. laeviceps* to locate food sources like nectar and pollen before employing visual cues to recognize flowers (Grüter, 2020; Raguso, 2008). In the case of citrus flowers, 110 volatile compounds have been identified from nine different species (Azam et al., 2013). Given the high abundance of volatile compounds in citrus flowers, they represent an excellent choice for studying the mechanisms underlying the attraction of *T. laeviceps*. Based on a previous study, the stingless bee *Scaptotrigona pectoralis* prefers orange flower extract over lemon flower extract (Grajales-Conesa et al., 2012). Furthermore, visual preferences among stingless bee species vary. For instance, species like *Partamona helleri* and *Tetragonula carbonaria* exhibit specific color preferences, including red, white, and yellow (Dyer et al., 2019; Koethe et al., 2018), while *Melipona bicolor* does not show a preference for flower color (Koethe et al., 2018).

This study aims to identify the factors primarily affecting the attraction of *T. laeviceps* in indoor experiments using olfactory and visual cues. Additionally, we investigated the effects of microclimate conditions during experiments by monitoring temperature, relative humidity, and light intensity as crucial factors. Furthermore, the volatile compounds released from the essential oils were analyzed using Gas Chromatograph – Mass Spectrometry (GC-MS). Through the experiments, we considered the following hypothesis: i) orange volatile compounds are more attractive to *T. laeviceps* than lemon volatile compounds. ii) microclimate conditions influence the number of visits. iii) *T. laeviceps* exhibits specific color preferences. Thus, this study provides more insights into the effects of olfactory and visual cues and microclimate conditions on the attractiveness behavior of *T. laeviceps*.

Material and methods

Behavior preparation

Behavior experiments on *T. laeviceps* were conducted at the stingless bee house (SBH) within the School of Life Sciences and Technology, Institut Teknologi Bandung, Indonesia. Microclimate conditions, including temperature, relative humidity, and light intensity, were measured using the Data Logger HOBO U10-003 during observations in March 2023. Four *T. laeviceps* colonies were obtained from local beekeepers in Banjaran, West Java, Indonesia, each consisting of an average of 400 to 600 adult worker bees. They were placed in the SBH two weeks before the observation period. Essential oils were used as olfactory cues, and artificial flowers were used as visual cues due to the limited availability of citrus flowers. The experiment included six-choice assays using artificial flowers (red and white color) as visual cues and citrus essential oils (*Citrus reticula* and *Citrus limon*) diluted in solvent (ethanol) as the odor source.

Behavior experiments and analysis

The essential oils of orange and lemon were diluted in ethanol at a ratio of 1/100. Subsequently, 20 µL of each treatment solution was placed in 2 mL vials. Artificial flowers were positioned on top of the vial. One hour before the commencement of observations, each treatment vial was positioned within the Stingless Bee House (Fig 1). Observations were conducted hourly, starting from 7:00 and continuing until 16:00. Each observation period lasted 30 minutes. *T. laeviceps* visits were recorded when the bee was within a 1 cm proximity of the test compound. We assessed sample attractiveness through the attraction index (%) using the Equation outlined by Sathiyaseelan et al. (2023):

$$\textit{Attraction index (\%)} = \frac{T - CN}{N} \times 100\%$$

where T is the number of *T. laeviceps* attracted in treatment, C is the number of *T. laeviceps* attracted in treatment, and C is the total number of *T. laeviceps* attracted in samples.

All collected data was tested for normality and homogeneity of variance, and no data transformation was deemed necessary. The olfactory and visual cue preferences of *T. laeviceps* were assessed through two-way ANOVA with Tukey's Honestly Significant Difference (HSD) test. The effects of microclimate variables on the number of *T. laeviceps* visits to the test compounds were examined using Pearson correlation (*r*) and Principal Component Analysis (PCA). These analyses were conducted using R version 4.3.2. (R Core Development Team, 2023).

Analysis of volatile compounds

Volatile components released from the essential oils were collected using dynamic headspace collection. We prepared the samples by diluting orange and lemon essential oils with ethyl acetate at ratios of 1/100 and 1/200, respectively. Subsequently, 100 µL of each sample was placed in a 5 mL vial for 10 minutes. Volatile components filled in the vial were collected using NeedlEx (fatty acids type) (Shinwa, Kyoto, Japan). Gas Chromatograph – Mass Spectrometry (GC-MS) analyses were performed on a GCMS-QP2010 Plus (Shimadzu, Kyoto, Japan) equipped with a capillary column (HP-1MS, 25 m × 0.20 mm, 0.33 µm film thickness, Agilent Technologies, CA, USA) using helium as the carrier gas.

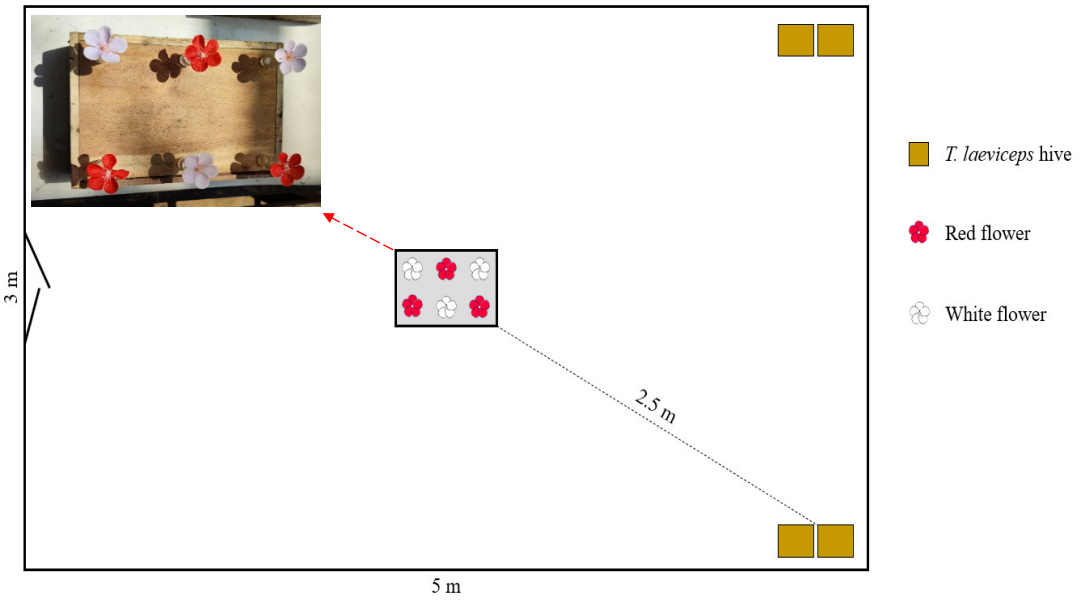

Fig 1. Behavior experiments design in stingless bee house.

The temperature of the GC oven was programmed to increase from 60 °C (2 min holding) to 290 °C at a rate of 10 °C/min. The needle of NeedlEx was exposed at the injection tip, and the absorbed volatiles were injected into an injection port at 250 °C by extruding 0.8 mL of nitrogen using a syringe. Otherwise, authentic samples were directly injected into the injection port. The volatile compounds were identified by comparing their retention times and mass spectra with those of corresponding authentic samples (Table S2). Alternatively, a volatile was putatively identified by comparison of its mass spectrum with a mass spectrum library (NIST11.lib).

Results

We observed the behavior of the stingless bee *Tetragonula laeviceps* that visited the test samples from 8:00 to 15:00 for 13 days of experiments (Table S1). The behavior pattern of *T. laeviceps* increased from 8:00 to 11:00, followed by a decrease until 15:00 (Fig 2). The highest number of visits was at 11:00, with 32 bees visiting orange essential oil ($p < 0.05$), followed by 14 bees visiting lemon essential oil ($p < 0.05$), and two bees visiting solvent treatment ($p < 0.05$). Furthermore, there was no significant difference in the number of visits between red and white artificial flowers ($p > 0.05$).

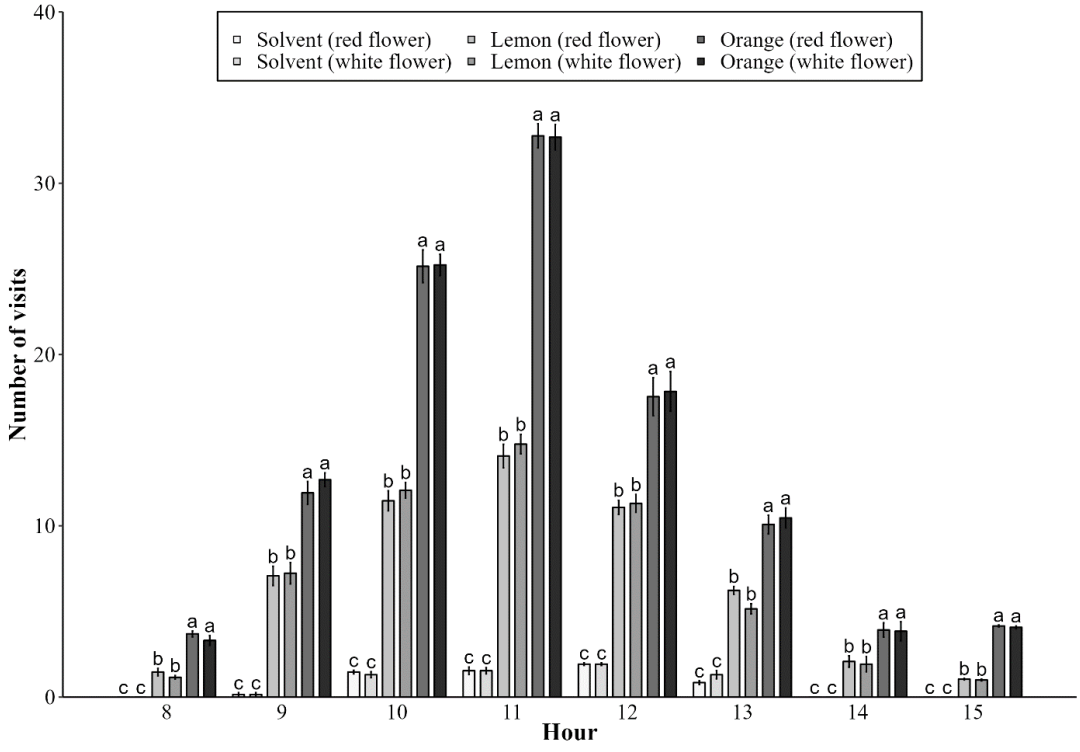

Fig 2. The average numbers of *Tetragonula laeviceps* visits to six test samples (mean ± SD) followed different letters within a bar indicate significant differences ($p < 0.05$) by two-way ANOVA with Tukey's HSD test ($N = 13$).

Furthermore, we analyzed the daily behavior of *T. laeviceps* visited to the test samples. The daily average number of visits to the test compounds varied significantly between treatments (Table 1). The orange essential oil resulted in the highest *T. laeviceps* visits ($p < 0.05$), followed by the lemon essential oil ($p < 0.05$) and the solvent treatment ($p < 0.05$). Interestingly, red and white artificial flowers did not affect *T. laeviceps* visits ($p > 0.05$). The highest percentage of index attraction is an orange essential oil with a white flower at 29.86%, followed by orange essential oil with a red flower at 29.72%, lemon essential oil with a red flower at 14.71%, and lemon essential oil with a white flower at 14.66%.

Table 1. The daily average number of *Tetragonula laeviceps* visits the test samples.

No	Treatment	Artificial flowers	
		Red flower (stingless bees)	**White flower** (stingless bees)
1	Solvent	6.08 ± 0.18^{c}	6.23 ± 0.13^{c}
2	Lemon essential oils	55.31 ± 0.28^{b}	55.31 ± 0.25^{b}
3	Orange essential oils	105.54 ± 1.01^{a}	106.15 ± 1.13^{a}

Data are means ± SD followed different letters within a column and row indicate treatment significant differences ($p < 0.05$) by two-way ANOVA with Tukey's HSD test ($N = 13$).

Next, we analyzed the behavior under microclimate conditions, including temperature, relative humidity, and light intensity. The behavior experiments observed no significant differences in the daily microclimate conditions for temperature, relative humidity, and light intensity ($p > 0.05$). Temperature and light intensity exhibit a similar pattern to the behavior of *T. laeviceps* visited samples, while relative humidity shows an opposite pattern (Fig 3). The average number of *T. laeviceps* visits to the test samples demonstrated correlations with temperature, relative humidity, and light intensity. Specifically, a high positive correlation was observed between the number of visits and temperature ($r = 0.75$, $p < 0.05$). At the same time, there was a moderate positive correlation between the number of visits and light intensity ($r = 0.51$, $p < 0.05$). Conversely, a moderate negative correlation was identified between the number of visits and relative humidity ($r = -0.52$, $p < 0.05$).

The principal component analysis (PCA) assessed which component significantly influenced the number of *T. laeviceps* visits to the test samples (Fig 4). The results indicate that temperature ($cos2 = 0.32$) has the closest relationship to the number of visits ($cos2 = 0.33$). Therefore, temperature influences *T. laeviceps* visits to the test samples most, followed by light intensity ($cos2 = 0.49$) and relative humidity ($cos2 = 0.53$).

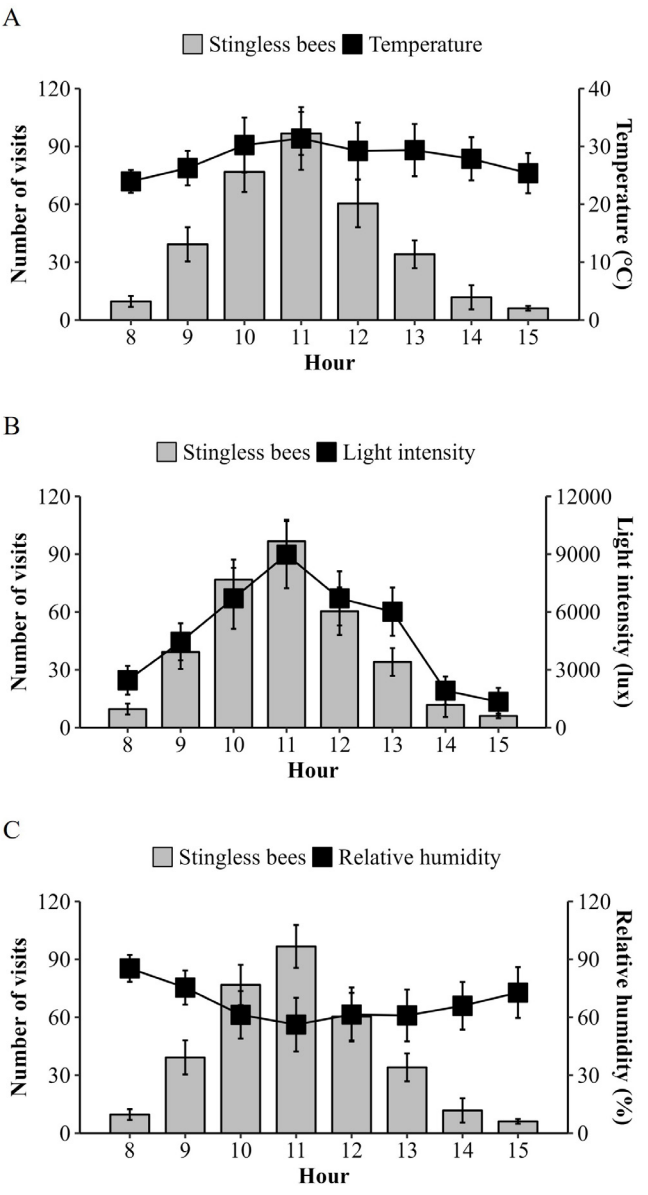

Fig 3. Comparison the number of visits with microclimate conditions. **A:** temperature; **B:** light intensity; **C:** relative humidity.

Since we observed that *T. laeviceps* were more attracted to artificial flowers treated with orange essential oil than those treated with lemon essential oils, their volatile components were analyzed using GC-MS. The two essential oils shared common volatile compounds but showed different peak intensities for these compounds (Fig 5). Among these essential oils, β-myrcene, D-limonene, linalool, α-terpineol, β-citral, α-citral, and β-caryophyllene were identified by comparing their retention times and mass spectra with those of the corresponding authentic samples. In addition, β-ocimene was putatively identified by comparing its mass spectrum with a mass spectrum library (Fig S1, Table S3). The main predominant compounds of orange essential oil are linalool and α-citral, while D-limonene and β-caryophyllene are the main compounds in the lemon essential oil.

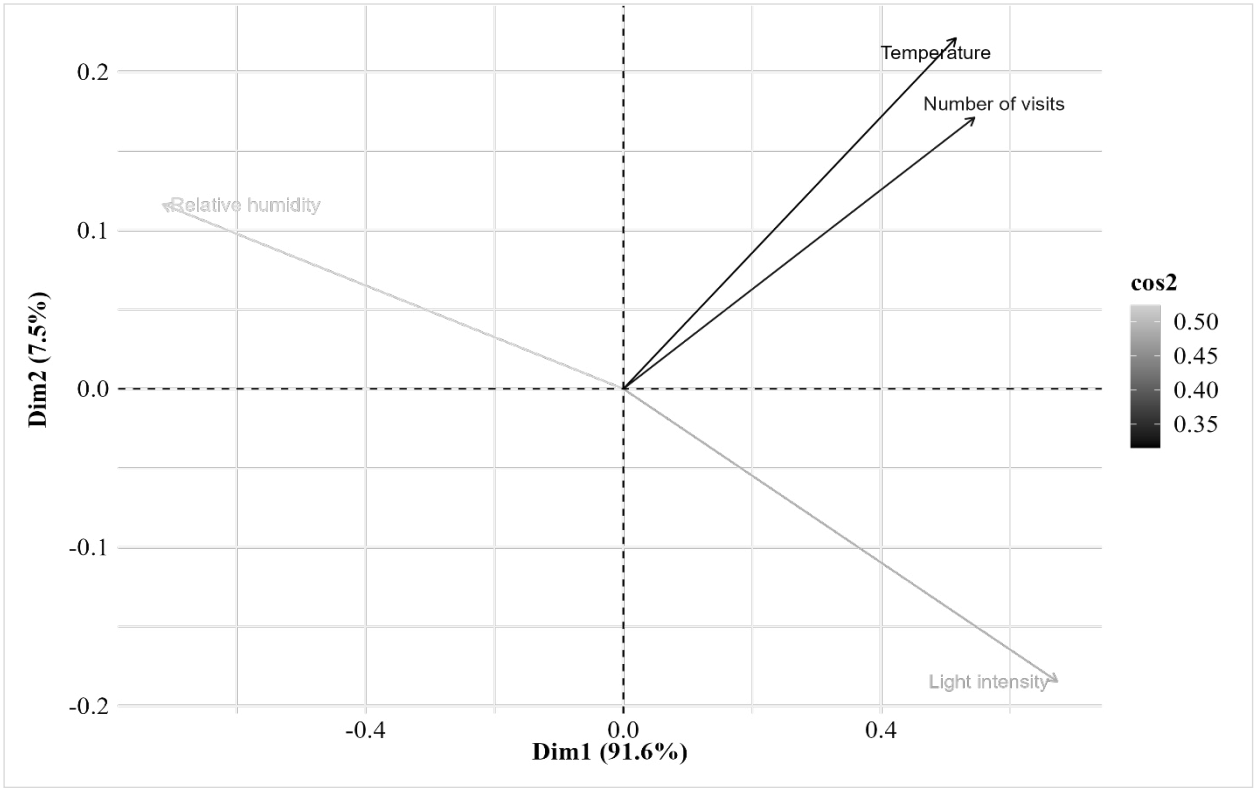

Fig 4. Principal component analysis between the microclimate conditions with number of *Tetragonula laeviceps* visits to the test samples.

Discussion

In the present study, we investigated the effects of various factors that attract *T. laeviceps* in indoor experiments. We observed that the behavioral pattern of *T. laeviceps* responding to the test samples is closely tied to its daily foraging behavior, primarily driven by its search for nectar and pollen. Interestingly, *T. laeviceps* exhibits a foraging schedule distinct from other insect pollinators, such as honey bees and carpenter bees, which typically start their foraging activities

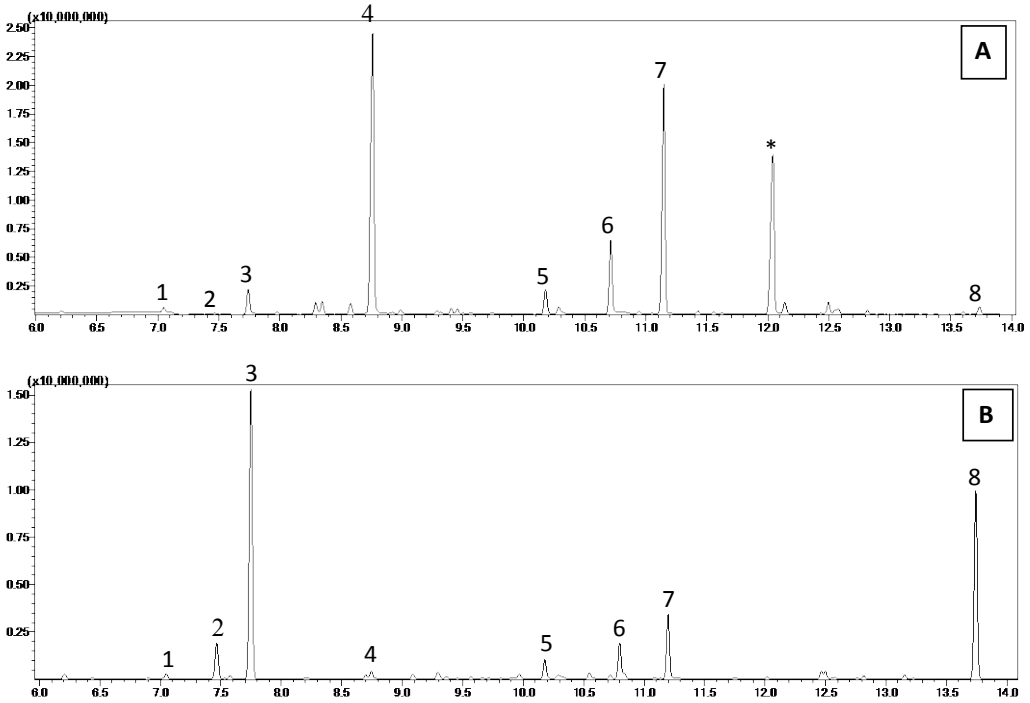

Fig 5. The identifications of volatile compounds from citrus essential oils. **A**: Orange (*Citrus reticulata*); **B:** lemon (*Citrus limon*) (Compounds name: 1. β-Myrcene, 2. β-Ocimene, 3. D-Limonene, 4. Linalool, 5. α-Terpineol, 6. β-Citral, 7. α-Citral, 8. β-Caryophyllene, *. Glycerine).

early in the morning (Hall et al., 2020; Putra et al., 2014). *T. laeviceps* initiates its foraging activities early in the morning, focusing initially on collecting resin for nest construction and protection against potential predators. Subsequently, it shifts its focus to collect nectar and pollen for the colony. This unique foraging behavior distinguishes *T. laeviceps* from other stingless bee species, including *Heterotrigona itama*, *Tetragonula carbonaria*, and *Tetragonula iridipennis*, which commence their resin and pollen collection activities later in the day (Hall et al., 2020; Kishan Tej et al., 2017; Putra et al., 2014; Trianto & Purwanto, 2022).

Microclimate conditions, including temperature, relative humidity, and light intensity, are crucial factors influencing the foraging activity of pollinators as they search for pollen, nectar, and resin (Aizen et al., 2019; Garibaldi et al., 2011; Polatto et al., 2014). These factors are significant for *T. laeviceps* (Abduh et al., 2023). We observed a positive correlation between the number of *T. laeviceps* visits to the test samples for temperature ($r = 0.75$) and light intensity ($r = 0.51$). In contrast, a negative correlation exists with relative humidity ($r = -0.52$). These findings are consistent with previous studies that reported a positive correlation between the number of pollinators visiting flowers and temperature and light intensity but a negative correlation with relative humidity in the field (Cholis et al., 2020; Polatto et al., 2014; Taha et al., 2016). Temperature is a crucial factor in influencing the number of *T. laeviceps* visits, and this is supported by previous studies (Gallagher & Campbell, 2020; Layek et al., 2020; Polatto et al., 2014; Taha et al., 2016). The stingless bee *Plebeia* aff. *flavocincta* highly relies on elevated temperatures for its activities outside the nest (Barbosa et al., 2020). This dependence is due to the ability of stingless bees to perceive changes in environmental temperature around their nest directly. These stingless bees are sensitive to changes in relative humidity and light intensity in their surroundings when they leave the nest. These conditions create an optimal microclimate that significantly influences the activity of stingless bees in their search for resources.

This study focuses on the effects of color and volatile compounds in the behavioral test. The color of the artificial flowers had no discernible impact on the number of *T. laeviceps* visits, indicating that *T. laeviceps* probably does not exhibit color preferences. This observation aligns with findings for other stingless bee species, such as *M. bicolor*, which also lacks color preferences (Koethe et al., 2018). On the contrary, *T. iridipennis* displays spontaneous color behavior when visiting flowers (Balamurali et al., 2018). Furthermore, like *P. helleri* and *T. carbonaria*, some stingless bee species, like honey bees and bumble bees, exhibit color preferences (Dyer et al., 2019; Koethe et al., 2018). *T. laeviceps* attraction to orange flowers in agroecosystems is influenced by olfactory and visual cues and the comprehensive assessment of rewards it receives from visiting these flowers (Dyer et al., 2019; Koethe et al., 2018). Furthermore, in agroecosystems, pollinators can gather and evaluate information from a wide range of visual and olfactory cues emitted by various organisms (Kantsa et al., 2017). Visual and olfactory cues synergistically create attractiveness for insects such as honey bees (Rachersberger et al., 2019).

The attractiveness of *T. laeviceps* to orange essential oil is relatively high (30%), which indicates that *T. laeviceps* has an interest in certain compounds. The different numbers of *T. laeviceps* visiting the test samples may be attributed to the differences in the abundance of major volatile compounds. Although orange and lemon essential oils share the same eight major volatile compounds, their concentrations are distinctly different. This variance in volatile compound concentration could influence *T. laeviceps*, leading it to visit orange essential oils more frequently than lemon. Of these significant volatile compounds, linalool is the most concentrated in the orange essential oils. Notably, linalool is also the predominant volatile compound in orange flowers (Azam et al., 2013). Linalool is widely recognized as a terpenoid with significant relevance in plant-insect interactions, serving both as an attractant and a repellent (Beck et al., 2017; Feng et al., 2022; Raguso, 2008; Zhang et al., 2023). Furthermore, linalool has been identified as an attractant for various pollinators, including honey bees (Malerbo-Souza et al., 2004), bumble bees (Klatt et al., 2013), and stingless bees *Tetragonisca angustula* (Mc Cabe & Farina, 2010). Further research is required to specifically test compounds such as linalool as potential attractants for *T. laeviceps*.

Conclusion

Orange essential oil was more attractive to *T. laeviceps* than lemon essential oil, which agrees with the initial hypothesis. Furthermore, the hypothesis that the number of *T. laeviceps* visits to the test samples would increase with increasing temperature, light intensity, and decreasing relative humidity was also confirmed, with temperature being identified as the most influential factor in foraging behavior. However, *T. laeviceps* did not exhibit a specific color preference, leading to the rejection of the initial hypothesis. Orange and lemon essential oils contained eight terpene compounds, but the main constituents were different. Linalool and α-citral were predominant in the orange essential oil, while D-limonene and β-caryophyllene were the main components in the lemon essential oil. The characteristic terpenes could be the attractants to *T. laeviceps*.

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Authors' Contribution

MAN: Conceptualization, methodology, formal analysis, investigation, writing-original draft, visualization.
MYA: Writing-review and editing, supervision.
HO: Conceptualization, methodology, investigation, writing-review and editing.
ADP: Writing-review and editing, supervision.

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