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Climatic fluctuations alter the preference of stingless bees (Apidae, Meliponini) towards food contaminated with acephate and glyphosate

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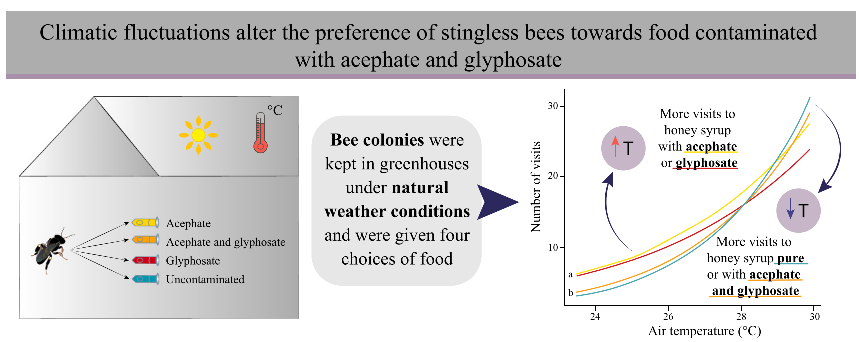
HIGHLIGHTS

- The risk of pesticide exposure in the field depends on the behavior of bees.
- Free-flying bees could choose between food contaminated or not with agrochemicals.
- Experiments were conducted in greenhouses under field realistic conditions.
- Bees displayed temperature-dependent preference for agrochemical-contaminated diets.
- Pesticide residues in nectar can attract bees to contaminated food sources.

GRAPHICAL ABSTRACT



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ABSTRACT

The global decline of pollinators has become a major concern for the scientific community, policymakers, and the general public. Among the main drivers of diminishing bee populations is the widespread use of agrochemicals. To gain a comprehensive understanding of the foraging dynamics of bees at agrochemical-contaminated areas, it is essential to consider both environmental conditions and the specific foraging ecology of bee species. For the first time, we conducted a semi-field study to investigate whether stingless bees exhibit a preference for food contaminated with agrochemicals compared to non- contaminated food, under natural weather conditions. Colonies of *Plebeia lucii* Moure, 2004 were placed in a greenhouse and subjected to a preference test, where bees were given the freedom to choose between contaminated or non-contaminated food sources following a preliminary training period. Within the greenhouse, we placed feeders containing realistic concentrations of an insecticide (acephate: 2 mg a.i./L), a herbicide (glyphosate: 31.3 mg a.i./L), or a mixture of both, alongside non-contaminated food. Environmental variables (temperature, humidity, and light intensity) were monitored throughout the experiment. At higher temperatures, the foragers preferred food containing the mixture of both agrochemicals or uncontaminated food over the other treatments. At lower temperatures, by contrast, the bees

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preferred food laced with a single agrochemical (acephate or glyphosate) over uncontaminated food or the agrochemical mixture. Our findings indicate that agrochemical residues in nectar pose a significant threat to *P. lucii* colonies, as foragers do not actively avoid contaminated food, despite the detrimental effects of acephate and glyphosate on bees. Furthermore, we demonstrate that even minor, natural fluctuations in environmental conditions can alter the colony exposure risk. Despite the interplay between temperature and bees' preference for contaminated food, foragers consistently collected contaminated food containing both agrochemicals, whether isolated or in combination, throughout the whole experiment.

1. Introduction

Over the past decade, the global decline of pollinators, particularly managed and wild bees, has garnered significant attention from the scientific community, policymakers, and the general public (Sluijs and Vaage, 2016; Stout and Dicks, 2022). A primary driver behind this decline is the frequent and improper use of agrochemicals (Goulson et al., 2015). Bees, while foraging for food in both crop fields and native habitats nearby or within agricultural areas, are susceptible to accidental exposure to agrochemicals, which can have detrimental effects on most species, ranging from sublethal to lethal effects, even if they are of biological origin (Marques et al., 2020; Bernardes et al., 2022; Ward et al., 2022; Cappa et al., 2022; Pan et al., 2023). Foraging individuals may pick up agrochemicals by passing through airborne spray drifts, by landing on leaves and flowers with residues, or by collecting contaminated nectar and pollen (Ward et al., 2022). Of particular concern is the latter case, as bees can transfer these agrochemical-contaminated nectar and pollen to their brood. The consequent chronic exposure of immature individuals to sublethal doses leads to developmental deficits, negatively impacting adult survival, pathogen susceptibility, and cognition (Zhu et al., 2014; Doublet et al., 2015; Tan et al., 2017; Dorneles et al., 2021). However, whether and to what extent foragers uptake agrochemicals with their food depends on various factors, including the species-specific foraging behavior of bees (Tschoeke et al., 2019; Boff et al., 2020), the type of agrochemical (Supplementary Material, Table S1), and the bees' capacity to perceive specific toxins (Kessler et al., 2015; Mubin et al., 2022; Farnan et al., 2023).

As many agrochemicals are neurotoxins (Desneux et al., 2007; Goulson et al., 2015), both acute and chronic exposure during food collection can result in behavioral deficits in foragers, including cognitive dysfunction (Siviter et al., 2018; Carlesso et al., 2020; Di Noi et al., 2024), reduced navigational skills (Henry et al., 2012), and altered responses to odor cues (Thompson, 2003). Of particular interest are changes in preference towards agrochemical-contaminated food sources over time. Recent studies have documented increasing attractancy or increasing repellency for different bee species (Arce et al., 2018; Tschoeke et al., 2019; Thompson et al., 2022). However, in some bee species-agrochemical combinations, no changes in resource attractiveness over time was observed (Tschoeke et al., 2019; Muth et al., 2020).

An important parameter that requires consideration when investigating potential shifts in bee preference towards agrochemical-contaminated food is the species' foraging ecology. Beyond inherent differences in foraging strategies among species (e.g., Michener, 1974), environmental factors such as light intensity, air temperature, and solar radiation may affect the bees' foraging choices (Biesmeijer et al., 1999a, 1999b; Teixeira and Campos, 2005; Streinzer et al., 2016). Preferences for specific fragrances, in particular, have been observed to vary across seasons (Ackermann, 1989) and also vary with increasing temperature (Russell and McFrederick, 2022). Thus, environmental conditions and bee species-specific foraging ecology must be considered to gain a comprehensive understanding of the foraging dynamics of bees at agrochemical-contaminated resources.

In this study, we investigated potential variations in the effect of food contaminated with agrochemicals on the foraging preferences of *Plebeia lucii* Moure 2004 (Apidae, Meliponini) under semi-field conditions in managed greenhouses. Over a three-day period, foragers of this stingless bee species were given the freedom to choose between food sources containing sublethal doses of acephate (insecticide), glypohsate (herbicide), a mixture of both (common in tank mixtures), or pure sugar syrup. Our study aimed to answer the following questions: (1) Do bees exhibit preferences for any of the offered agrochemical-contaminated food types in comparison to the uncontaminated food? (2) Do these preferences change over time (within a days' foraging period or across the three days of exposure)? (3) Can variations in foraging preferences be attributed to variations in environmental conditions (temperature, light intensity)?

2. Material and methods

2.1. Bees and agrochemicals

We studied potential changes in the attractiveness of food contaminated with agrochemicals using three well-established and queenright colonies of *Plebeia lucii* Moure 2004 (Apidae, Meliponini). These colonies were kept in wooden boxes (12 × 9 × 9 cm). Prior to the experiments, the nests were maintained in the meliponary of the Universidade Federal de Viçosa (UFV), Brazil, in an area surrounded by fragments of Atlantic Rainforest (20°45′43.7″ S; 42°51′44.9″ W). The experiments were performed between August and September 2021. During these months, which follow the local winter season, *P. lucii* colonies typically exhibit increased foraging activity, and colony populations rise due to a heightened egg-laying activity of the queens.

The agrochemicals chosen for the experiments were the insecticide acephate (ACE) and the fungicide glyphosate (GLY). We used field-realistic doses of both agrochemicals, based on previous reports of the presence of acephate (2.0 mg a.i./L; Fiedler, 1987) and glyphosate (31.3 mg a.i./L; Thompson et al., 2014) in nectar of treated crops. These agrochemical concentrations are sublethal for *P. lucii* (Ferreira et al., 2023) and are notably low, particularly when compared to the doses recommended by the Brazilian Ministry of Agriculture, which are over 250 times higher (ACE: 562.5 mg/L; GLY and 11,125.0 mg glyphosate/L) for the use of both agrochemicals on *Citrus* crops (MAPA, 2023). For the preparation of the experimental treatments, we utilized the commercial formulation Cefanol® (ACE 750 g a.i./kg, soluble powder, Sipcam Nichino Brasil S.A.) and Roundup Original DI ® (GLY 445 g a.i./L, soluble concentrate, Monsanto do Brasil Ltda - São Paulo). The final concentration of the agrochemicals in the solutions was not confirmed analytically.

2.2. Agrochemical preference tests

For the experiments, we transferred the nests to a small insect-proof greenhouse (2 × 2 × 2 m^3), located outdoors in an area protected from the rain. Sunlight exposure induced a semi-natural fluctuation in daily temperature (23.5–29.9 °C), relative humidity (38–62 %), and light intensity (4310–13,080 lx) within the experimental enclosure. Foragers could freely forage inside the greenhouse, which was completely sealed to prevent bee escape and to eliminate interference from bees belonging to other colonies in the vicinity.

We introduced one colony at a time into the greenhouse for four consecutive days (Colony A: 27/08/2021–30/08/2021; Colony B: 31/08/2021–03/09/2021; Colony C: 04/09/2021–07/09/2021). On the first day (pre-trials), foragers were trained to visit feeders containing pure honey syrup (1:1 *v*/v honey and distilled water solution) at the experimental setup location, a table positioned at a distance of 1.5 m from the nest entrance. From the second to the fourth day (three days of consecutive trials), we placed four feeders equidistantly on the table, at positions “P1”, “P2”, “P3”, and “P4”, each containing one of the following treatments: (i) uncontaminated honey syrup (control), (ii) honey syrup with 2.0 mg a.i./L acephate, (iii) honey syrup with 31.3 mg a.i./L glyphosate, and (iv) honey syrup containing a mixture of 2.0 mg a.i./L acephate and 31.3 mg a.i./L glyphosate. The bees had access to the feeders for 2.5 h/day, during which the feeders were randomly repositioned at every 10 min to avoid position biases (adapted from Arce et al., 2018; see Supplemental Material). Throughout the experiment, the activity at the feeders was recorded using a digital video camera (Nikon D3500®, 18–55 mm lenses, 60 fps, 1920 × 1080 pixels) to determine the number of bees visiting each treatment at each 10 min time interval. Only events in which a bee landed at a feeder and took up honey syrup (identified through the proboscis's extension into the food) were considered as visits. Foragers who landed at the feeder but left without collecting food were not included in the analysis. After each experimental day, the feeders were cleaned with alcohol 70 % to eliminate chemical clues deposited by the bees. Video-recordings started as soon as the first bees arrived at the feeders (between 11:00 and 12:30). The first arrival of bees was considered as the onset of the experiment (time = 0.0 h). Each time the feeders were repositioned (every 10 min), we recorded air temperature (TA) and relative humidity (RH) using a digital thermo-hygrometer (K29—5070H - Kasvi®) and the light intensity (LI) using a digital lux meter (MLM-1011 - Minipa®).

2.3. Data analysis

To analyze the effects of the different food treatments and the environmental fluctuations on the bees' behavior, we used generalized linear mixed models (GLMM). We used the R-software package “GGally” (Schloerke et al., 2021) to estimate the correlations between environment parameters (TA, RH, LI). Owing to the high correlation between air temperature and relative humidity ($r = -0.8$), RH was excluded from further analysis. The correlation between air temperature and light intensity was weak ($r < 0.39$), so both environmental parameters were maintained in the models. We performed GLMMs to determine how feeder choice (response variable: “number of visits”) is influenced by agrochemical treatment (categorical explanatory variable: uncontaminated (CO), acephate (ACE), glyphosate (GLY), and acephate and glyphosate mixture (ACE+GLY)), air temperature (numerical explanatory variable) or light intensity (numerical explanatory variable) and the interaction between the explanatory variables (treatment × TA × LI). We applied a backward model selection approach to identify the simplest fitted models, using the likelihood ratio test. Therefore, the statistical significance was tested by simplifying the model gradually, removing non-significant explanatory variable. Colony identity was included as random intercept. Significant differences between treatments were compared by means of contrast analyses.

We applied GLMMs to assess how feeder preference is influenced by agrochemical treatment (categorical explanatory variable: CO, ACE, GLY, ACE+GLY), duration of exposure (numerical explanatory variables: “time relative to the onset of the experiment each day”, min = 0.0 h; maximum = 2.5 h, or “day of experiment”, days 1 to 3) and the interaction between them (treatment × duration of exposure). Colony identity was included as random intercept. The analyses accounted for repeated measures by fitting a random slope using the duration of exposure (day or time) as continuous random variable.

The potential bias of the feeders' position was evaluated through a GLMM using “number of visits” as response variable, “treatment” (CO, ACE, GLY, ACE+GLY) and “feeder position” (“P1”, “P2”, “P3”, and “P4”) as categorical explanatory variables, and “colony” as random effect (random intercept). Additionally, to ensure that no feeder with a given treatment was placed in a position more often than the others, and that any feeder preference was not influenced by position, we measured the correlation between position and the treatments by means of a Pearson's Chi-squared in the “janitor” package (Firke, 2021).

We used negative binomial distribution in all GLMMs using the packages “lme4” (Bates et al., 2015) and “MASS” (Venables and Ripley, 2002). All analyzes were performed using the R software (version 4.3.2; R Core Team, 2023), and graphs were generated using the packages “ggplot2” (Wickham, 2016) and “plot3D” (Soetaert, 2021).

3. Results

The relative preference for agrochemical-contaminated food varied with ambient temperature. *P. lucii* foragers were significantly attracted to honey syrup treated with sublethal doses of acephate and glyphosate at lower temperatures, whereas at warmer conditions they preferred non-treated honey syrup and the honey syrup treated with the agrochemical mixture of acephate and glyphosate ($\chi^2 = 9.909$, $df = 3$, $P = 0.019$) (Fig. 1). There were no differences between the number of visits to the ACE and GLY feeders ($\chi^2 = 0.643$, $df = 2$, $P = 0.725$) and between the CO and ACE+GLY feeders ($\chi^2 = 0.578$, $df = 2$, $P = 0.749$) (Fig. 1).

The bees' attraction towards a specific food source remained consistent throughout the 2.5 h of food presentation ($\chi^2 = 4.738$, df = 3, $P = 0.192$). Also, there were no significant differences between the treatments in the number of visits observed between the three days of our experiment ($\chi^2 = 0.088$, df = 3, $P = 0.993$).

In contrast to ambient temperature, changes in light intensity had no significant influence on the variation in the number of visits to feeders from different treatments ($\chi^2 = 5.573$, $df = 3$, $P = 0.134$). However, the number of visits to all feeders, regardless the treatment, was affected by the interaction between light intensity and ambient temperature ($\chi^2 = 8.027$, $df = 1$, $P = 0.005$) (Fig. 2). Nevertheless, this interaction had no effect on the number of visits to feeders from different treatments, indicating no impact on the food preference of foragers ($\chi^2 = 6.724$, $df = 3$, $P = 0.081$).

Regardless of the treatment, the number of visits to a particular feeder was affected by its position ($\chi^2 = 218.4$, $df = 3$, $P < 0.001$) (Fig. 3). The position of the feeders was identified, from left to right, as “P1”, “P2”, “P3”, and “P4”. The bees preferred the feeders that were on the position “P1”, followed by feeders on position “P2”, which were more to the left in the greenhouse ($\chi^2 = 83.821$, $df = 1$, $P < 0.001$). The two feeders more to the right, “P3” and “P4”, had the same number of visits ($\chi^2 = 0.314$, $df = 1$, $P = 0.575$). Nonetheless, there was no correlation between position and feeder treatment ($\chi^2 = 14.238$, $df = 9$, $P = 0.114$) (Fig. 3), which shows that none of the feeders with a given treatment was allocated to a certain position more often than the others. Thus, the above described results were not based on the foragers' bias towards a certain feeder position.

4. Discussion

Our study provides the first evidence of a temperature-dependent variation in foraging preferences for agrochemical-contaminated food by bees, highlighting how environmental conditions can alter the exposure risk of stingless bees to different agrochemicals. These findings caution against drawing generalized conclusions about the attractiveness, repellency, or absence of effects of agrochemicals on bees without considering the thermal regime. So far, toxicological studies with bees exposed to agrochemical exposure were either performed at a particular temperature in a laboratory (Kessler et al., 2015; Mubin et al., 2022; Farnan et al., 2023), or within a range of temperatures both in the field and the laboratory, without accounting for potential variations in the bees' preferences (Bernardes et al., 2017; Stejskalová et al., 2021; Albacete et al., 2023). Often studies neglect to provide information about the thermal regime under which the research was conducted (Elliott et al., 1979; Sánchez et al., 2012; Gómez-Escobar et al., 2014;

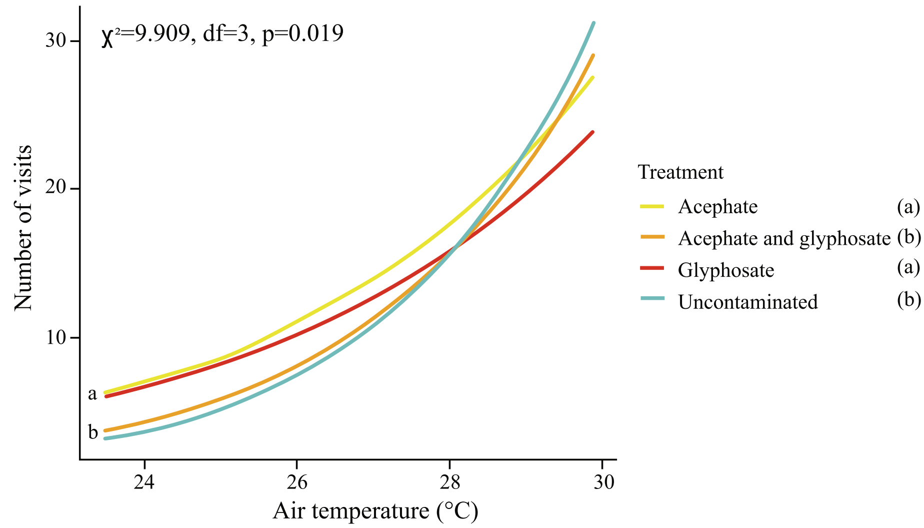

Fig. 1. Visits of *Plebeia lucii* foragers to each honey-syrup treatment under different temperatures. The regression lines represent each honey syrup treatment offered to the bees: uncontaminated, contaminated with acephate, contaminated with glyphosate, or contaminated with a mixture of acephate and glyphosate. Different letters represent significant difference between treatments according to the contrast analysis ($P < 0.05$). The experiment was undertaken with three stingless bee colonies, for three days per colony, and about 2.5 h a day. Observations were recorded every 10 min, resulting in 12 observations per day, for each of the four treatment feeders ($N = 432$).

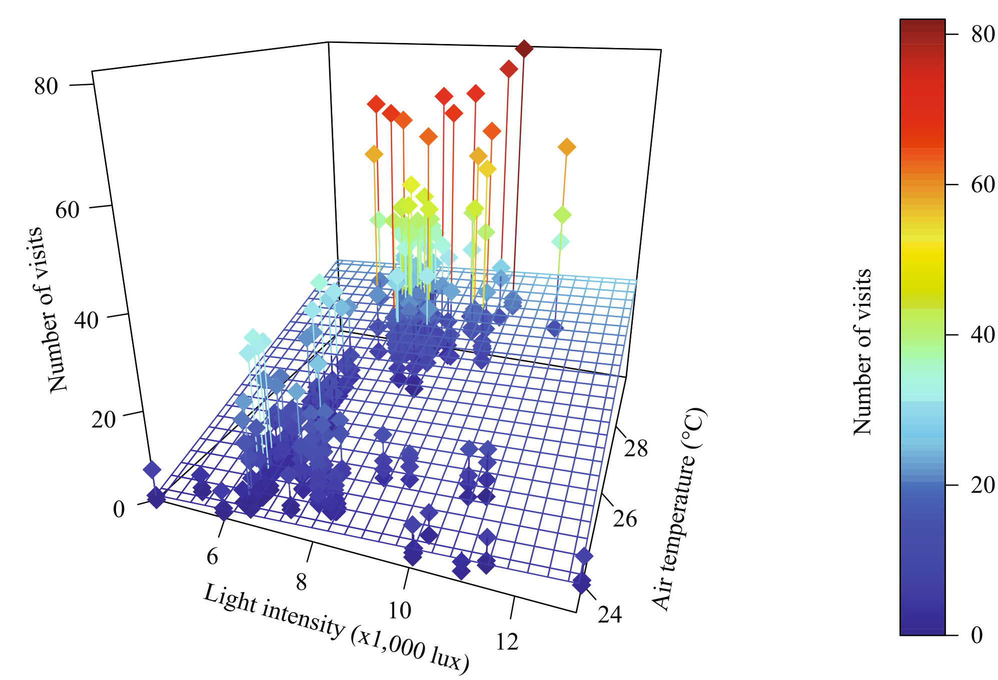

Fig. 2. Visits of *Plebeia lucii* foragers to honey-syrup feeders under different light intensity and temperatures. There was significant interaction between air temperature and light intensity in the number of visits when treatments were not considered ($P < 0.05$). The grid represents the linear model prediction of the effect of these environmental factors on the number of visits. The colored heat bar on the right represents the number of visits. The experiment was undertaken with three stingless bee colonies, for over three days per colony, and about 2.5 h a day. Observations were recorded every 10 min, resulting in 12 observations per day, for each of the four treatment feeders ($N = 432$).

Kang and Jung, 2017; Liao et al., 2017; Arce et al., 2018; Muth et al., 2020). Particularly worrying are instances of neutral reactions towards agrochemical-contaminated food (Table S1). Under lower temperatures, *Plebeia lucii* preferred food containing a single agrochemical over pure honey syrup or food containing a mixture of agrochemicals. At higher temperatures, the preference shifted, and foragers showed a higher attractance to uncontaminated food or food with the agrochemical mixture. Despite this temperature-dependent shift in preference, the bees visited the feeders with agrochemicals, isolated or mixed, under all temperatures.

Temperature fluctuations can alter nectar properties, such as microbiome composition, viscosity, warmth, sugar content, and sucrose concentration, consequently influencing the bees' food source preference (Whitney et al., 2008; Norgate et al., 2010; Nicolson et al., 2013; Tan et al., 2014; Russell and McFrederick, 2022). In this study, the only difference between the feeders offered to the bees was the presence or absence of acephate and glyphosate in the honey syrup. Therefore, any alterations of the honey syrup properties due to temperature

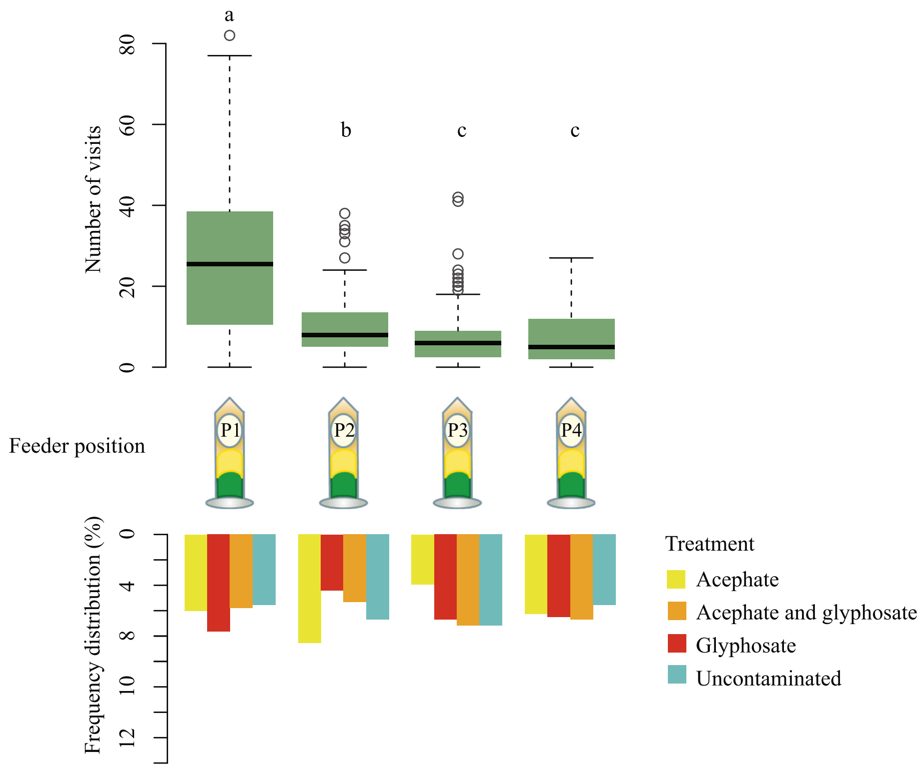

Fig. 3. Effect of position on the number of visits to the feeders. Number of visits to feeders at different positions (top) and percentage distribution of feeder treatment at each position (bottom), after random repositions every 10 min. Different letters represent significant differences between positions according to the contrast analysis ($P < 0.05$). There was no difference between the treatments with regard to the frequency distribution on positions. The experiment was undertaken with three stingless bee colonies, for three days per colony, and about 2.5 h a day. Observations were recorded every 10 min, resulting in 12 observations per day, for each of the four treatment feeders ($N = 432$).

fluctuations would likely be related to the agrochemical added to it.

The degradation of acephate and glyphosate can occur through different pathways depending on the environmental conditions, resulting in the production of different metabolites (Muskus et al., 2020; Lin et al., 2022; Muskus et al., 2022). Additionally, when two agrochemicals are mixed, one can interfere on the degradation process of the other (Fogg et al., 2003; Garcia-Muñoz et al., 2020). The degradation rate of agrochemicals in our trials could explain the temperature-dependent shift in the behavior of the foraging bees. Therefore, future studies should investigate whether different metabolites produced in the honey syrup after contamination with different agrochemicals could alter the preference of the bees.

Despite the observed temperature-dependent shift in preference, the foragers collected contaminated food over the entire temperature range throughout our study. Temperature fluctuations are generally known to exacerbate the negative impact of agrochemicals on insects (Ricupero et al., 2020; Silva et al., 2020; Verheyen et al., 2022; Alburaki et al., 2023; Albacete et al., 2023). Specifically, the toxicity of both acephate and glyphosate increases with temperature (Moulton et al., 1996; Baier et al., 2016; Stahlschmidt et al., 2022). The ingestion of sublethal concentrations of acephate and glyphosate can cause hyperactivity in animals (Behrend and Rypstra, 2018; Ivantsova et al., 2022), due to the inhibition or reduction of acetylcholinesterase (AchE) activity (Pohanka, 2011; Boily et al., 2013; Williamson et al., 2013; Yao et al., 2018). Since glyphosate and acephate do not have a known antagonistic effect (Pankey et al., 2004; Ma et al., 2016; Yao et al., 2018), their mixture would likely have a similar effect on AchE activity. Indeed, acephate and glyphosate cause alterations in the flight ability of *P. lucii* foragers (Ferreira et al., 2023), which can be related to their preference for food contaminated by these agrochemicals.

The absence of time-depending preference suggests that the bees' attraction to contaminated food was driven by an innate preference to some characteristic conferred to the food by the agrochemicals. Since all feeders had the same visual cues and food quantity, and feeder position did not interfere in the bees' behavior, it is likely that the attraction to contaminated feeders was mediated by olfactory cues. This hypothesis is reinforced by the fact that both naive and experienced foragers can locate food sources based on innate preference for specific olfactory cues, resulting in the observed immediate increase in the number of visits to the food source with the preferred odor (Milet-Pinheiro et al., 2012). Additionally, the release of odors from agrochemicals can be affected by the ambient temperature (Zaller et al., 2022). The lack of avoidance of acephate- and glyphosate-contaminated food observed in this study demonstrated a higher exposure risk to these agrochemicals, which are known to be detrimental to stingless bees (Macieira and Hebling-Beraldo, 1989; Seide et al., 2018; Nocelli et al., 2019; Diniz et al., 2020; Ferreira et al., 2023).

The preference of the bees was unaffected by light intensity, although its interaction with temperature affected the visitation frequency of *P. lucii*. Light intensity is known to alter the behavior of bees (Reber et al., 2015; Ngo et al., 2021) and the production of nectar in plants (Jones and Koptur, 2015; Fitch and Vandermeer, 2020). However, it is unclear to which extent light can affect nectar composition (Göttlinger and Lohaus, 2020), which could explain the lack of influence of this environmental condition on bee preference. Our results indicate that, despite altering the foraging activity of bees, light intensity does not affect their choice of food source.

5. Conclusions

In our study, we demonstrated that food contaminated with minute and realistic concentrations of acephate, glyphosate, and their mixture (Fiedler, 1987; Thompson et al., 2014) are attractive to stingless bees. As our study was conducted under natural weather fluctuations with direct colony exposure, along with the provision of different food choices for bees, we effectively simulated field conditions. Therefore, this study demonstrates that, under natural conditions, these stingless bees experience high exposure risk to agrochemicals applied not only on crops, but also the weeds nearby, which can harbor as much residue of these substances as the crops themselves (Long and Krupke, 2016; Ward et al., 2022). Furthermore, our data highlights that foragers collect and transport contaminated food to their colonies, which can cause intoxication and weakening of the whole colony (Gill et al., 2012; Whitehorn et al., 2012; Dively et al., 2015; Milone et al., 2021; Wueppenhorst et al., 2022).

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2024.175892.

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Compliance with ethical standards

The ARRIVE guidelines were followed in this study, and insects are not protected by the U.K. Animals (Scientific Procedures) Act, 1986. According to Brazilian legislation, we acquired two permissions to perform the present study (SISBIO permit no. 71998–0 and SISGEN permit no. AE230B3) and ethics approval is not necessary in researches conducted with invertebrates. In addition, our methods are consistent with commonly accepted norms of animal welfare.

CRediT authorship contribution statement

Lívia Maria Negrini Ferreira: Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Michael Hrncir:** Writing – review & editing, Visualization, Validation, Methodology, Formal analysis, Conceptualization. **Danilo Vieira de Almeida:** Investigation. **Rodrigo Cupertino Bernardes:** Visualization, Formal analysis. **Maria Augusta Pereira Lima:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Methodology, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

"The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request."

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