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When is it necessary to avoid your enemies? A stingless bee ignores aggressive competitor cues to explore food sources

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Abstract – Social insects have the ability to perform tasks in an organized way. Communication plays a key role in controlling these processes, and throughout evolution, these organisms developed a complex system for transferring information. Different stingless bee species use the same resource during foraging that could lead to an eventual competition. It is important for organisms to access the costs of confrontation with rival individuals and the energetic gain from foraging when exploiting a food source. Thus, the present work aimed to investigate behavioral responses in the foraging activity of *Plebeia droryana* Friese, 1900 in the presence of chemical and visual cues of *Trigona spinipes* Fabricius, 1793. Foragers of *P. droryana* were trained to visit artificial feeders with two different sugar concentrations and were exposed to chemical and visual cues of *T. spinipes* at different setups, but always separately. We also identified the cuticular hydrocarbons (CHCs) of *T. spinipes* foragers. Both visual and chemical cues from *T. spinipes* did not cause *P. droryana* to decrease its foraging activity at 50% sucrose concentration. We found that 40% concentration caused bees to reduce the foraging effort when faced with visual cues from *T. spinipes*. Thus, similar to other species, we found that *P. droryana* was attracted to the food source containing a 50% sugar solution regardless of the presence of *T. spinipes* chemical cues. Based on our results, we infer that food quality is the most important factor when *P. droryana* foragers are exploiting a food source.

chemical cues / stingless bees / foraging strategy / footprints

1. INTRODUCTION

In social insects, several foraging strategies exist, as individuals from the same colony work in different ways to maximize the benefits of this activity, which is considered one of the most important ways to assure colony survival (Ydenberg et al. 2007). Among them, the most commonly found is the active search for food, where individuals who move more have a greater chance of finding food patches (Davies et al.

2012). However, the final gain of foraging is the difference between the benefit of energy obtained from food and the costs of searching, handling, digesting, and escaping of potential risks (Ydenberg et al. 2007). Maximizing the energy input in foraging is the main point of the optimal foraging theory (MacArthur and Pianka 1966).

In stingless bees, resource collection is influenced by abiotic factors (Hilário et al. 2001; Nascimento and Nascimento 2012; Figueiredo-Mecca et al. 2013), e.g., the landscape, whether it is natural or altered, by the quantity and quality of food resources (Kaluza et al. 2016), etc. In addition, the energy cost during foraging is also important, and workers can fly longer distances if the resource is considered to be of good quality (Heinrich 1979; Cresswell et al. 2000).

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Stingless bees (Meliponini) are represented by more than 600 described species (Rasmussen and Cameron 2009, reviewed in Grüter 2020). Many species in this group often use the same food sources, which may result in interspecific competition (Johnson and Hubbell 1974; Biesmeijer et al. 1999; Hrncir and Maia-Silva 2013). The diversity of this group is reflected in the foraging strategies adopted by these different species (Biesmeijer and Slaa 2004; Jarau et al. 2009; Hrncir and Maia-Silva 2013). The three main factors that characterize Meliponini foraging strategies can be defined (i) based on group or solitary foraging, (ii) individual aggressiveness (absent or present), and (iii) individual reaction when faced with heterospecific foragers, which may lead to attraction or repulsion (Hrncir and Maia-Silva 2013). Regarding these factors, (i) is related to the biology of the species; and (ii) and (iii) involve the presence or absence of competitors at the food source, which can be conspecifics or not.

Flowers with better resources are more likely to be dominated and defended by more aggressive species or numerically dominated by group recruitment (Roubik 1989; Baumgartner and Roubik 1989; Hrncir and Maia-Silva 2013). As a result, bee species that feed on their own or in smaller groups tend to move to less disputed foraging locations, but also with lower food availability, or they try to access rich food sources earlier in the day than other species (Hrncir and Maia-Silva 2013). In the case of mass-flowering plants, there is greater food availability and the area is large enough, so there is no monopoly of resources for a single species, even in cases where mass recruitment occurs. In this food source, species that search alone or in smaller groups are undisturbed and may collect resources (Baumgartner and Roubik 1989; Hrncir and Maia-Silva 2013). The location of profitable sources of food during foraging flights leads to chemical signaling to guide colony foragers to locate the resource (Nieh 2004). Some of the compounds found in these odor cues are cuticular hydrocarbons (CHCs), which are mostly found on the cuticular surface and in some insect exocrine glands (Provost et al. 2008; Blomquist 2010). Their primary function is provides protection

against water loss, thermal regulation, and also acting as a barrier against microorganisms. Due to their structural complexity, they evolved in the form of contact pheromones, which are chemicals that are similar among individuals of the same species, and can stimulate reactions in insects of the same species (Rouault et al. 2004; Howard and Blomquist 2005; Blomquist 2010). The chemical cues left on the food sources, including CHCs, can be captured by a non-colony individual, conspecific or not, behaving like a spy to exploit the most profitable food sources, competition, and conflicts (Lichtenberg et al. 2011; Lichtenberg et al. 2014; Wang et al. 2016). Therefore, the most aggressive species are expected to dominate food sources already discovered by species that do not behave aggressively, according to the “dominance motivation hypothesis” (Lichtenberg et al. 2011).

To date, few studies have been conducted on the foraging behavior of stingless bees in food sources previously visited by other species. Although bees can discriminate the chemical compounds present between co-specific and heterospecific individuals, it is still little explored if they have the ability to recognize the chemical cues left in food sources (Jarau 2009). Previous works showed that foraging stingless bees passively leave chemical “footprints” on flowers and subsequent foragers may use them as indicators for previous heterospecific or conspecific flower visits (Jarau et al. 2004, 2005; Roselino et al. 2016). Thus, the knowledge about communication between different species can provide important information for understanding the evolution of chemical communication and foraging strategies in Meliponini, in addition to obtaining data on which chemical compounds are found in chemical cues left by *T. spinipes* at the explored food sources.

The aggressive behavior of the foragers of some *Trigona* species has been reported by Johnson and Hubbell (1974) and Roubik (1989). Due to the scarcity of resources available in nature, *Trigona spinipes* Fabricius 1793 is a species that displays aggressive behavior when foraging and can attack other stingless bees, especially in flowers. For instance, these meliponines attack *Apis mellifera* L., an invasive species, even before

landing on the flowers. Attacking behavior is characterized by biting the individual, and chasing may occur in mid-flight, which can end with the honey bee thrown to the ground (Minussi and Alves-dos-Santos 2007).

Despite not being an aggressive species, *Plebeia droryana* Friese 1900 has been seen attacking *T. spinipes* at artificial food sources (personal observation). This species utilizes a solitary foraging strategy, without food source communication between nestmates, but somehow, they find the exact location of a profitable food source (Lindauer and Kerr 1960; Hubbell and Johnson 1978; Nieh and Roubik 1998). After discovering a food source, some stingless bee species adjust their foraging frequency, their likelihood of recruitment, or their willingness to fight for a food source according to the quality of the given source (Johnson and Hubbell 1974; Biesmeijer et al. 1998; Jarau et al. 2009; Schorkopf et al. 2016). Similarly, the decision to return the next day (persistence) depends on a combination of the bees' ability to memorize the food source location and the information about the quality profitability of the given source (Seeley 1995; Biesmeijer et al. 1998; Biesmeijer and Slaa 2004; Al Toufaily et al. 2013). Furthermore, foraging research on *P. droryana* has shown that resource sucrose concentration influences the foraging activity of this species, which means that food quality is an important ecological factor (Peng et al. 2019).

Thus, this work was motivated by the opportunity to study the factors involved in the process of choosing the food source in the highly competitive environments in which these native bees live. Here, we study whether *P. droryana* foragers avoid food sources with chemical or visual cues of aggressive bee species. We tested the hypothesis that *P. droryana* would avoid food sources containing either visual or olfactory CHCs cues from *T. spinipes* in order to prevent energetically costly aggressive interactions with *T. spinipes* regardless of the quality of the food source in terms of sucrose concentration and the foraging cost in terms of distance to the feeder. Initially, we also identified the *T. spinipes* CHCs that were used during the experiments. Then, to conduct the experiments, we utilized separately each chemical

and visual cue from foragers of *T. spinipes* and analyzed if these cues have an influence on the foraging activity of *P. droryana*. We carried out two preference tests: experiment I, which included CHCs, visual cues, or control, and experiment II, which included visual cues or control at a lower sucrose concentration; both in the surroundings of the entrance of the colony.

2. MATERIAL AND METHODS

2.1. Study species and field site

We performed the experiments at the campus of the Universidade de São Paulo in Ribeirão Preto, Brazil. This area has a high diversity of wild stingless bee species (Cortopassi-Laurino et al. 2009; Freitas and Soares 2001). *P. droryana* was chosen due to its recurrent presence at our field site, and *T. spinipes* was used because of its aggressive behavior. In total, we studied five wooden box hives of *P. droryana* and one natural colony of *T. spinipes*. The *T. spinipes* colony used was located 30 m far away from the *P. droryana* colonies, with easy access that permitted the collection of individuals whenever necessary.

During each experimental bout, we used foragers from a single *P. droryana* colony. While the experiment with a focal colony was taking place, the other studied colonies were kept closed. In addition, individuals were paint marked to determine that most foragers usually came from the focal colony. We allowed a maximum of 5 to 10 non-painted individuals at the feeder due to time constraints to paint all of them and to not overtly disturb the experiment. All the tests were performed during a period of 6 weeks in March and April 2018. We counted the number of combs at each colony to assure that they were of the same relative size (from 6 to 7 combs). We only performed the experiments at a minimum ambient temperature of 25°C and a maximum of 32°C with clear sky and no strong wind presence. All data were collected between 9 a.m. and 12 p.m. During this period of time, there were no changes in the native vegetation that could impact the experiments, such as flowerings affecting resource availability.

2.2. Analysis of cuticular hydrocarbons of *T. spinipes*

We used Gas Chromatography combined with mass spectrometry (Shimadzu QP2010 plus) to analyze the *T. spinipes*' CHCs. The temperature started at 50 °C (5 min) and increased by 10 °C min⁻¹ to 310 °C. The final temperature was maintained for 15 min. This setting is the same as used by Schorkopf et al. (2007). The chromatograms were analyzed using GCMS Post-run Analysis software. The chemical compounds of the extract pool and footprints were identified. A retention index was calculated for each peak by using a standard solution of different synthetic linear alkanes (*n*-C21 – *n*-C40).

2.3. Experimental setup

The experimental setup was similar to those performed by Lichtenberg et al. (2011). The workers of *P. droryana* were conditioned to artificial feeders containing a 50% sucrose solution that was placed 1 cm from the nest entrance. This sucrose concentration was chosen because it is an attractive value for stingless bees, as they are known to collect nectar ranging from 5 to 67% w/w sugar, with an average concentration of 41% (Roubik et al. 1995). After a group of foragers was established in the feeder, it was slowly moved 5 m away from the colony entrance while the bees were still collecting the solution. Although *P. droryana* is a species that does not recruit for food sources, it was possible to train them for collecting food at the artificial feeders, because the bees are able to learn the new location of each respective feeder when returning to their nest (Von Frisch and Chadwick 1967; Nieh 2004). In addition, an individual forager tends to revisit the same food source after it has been successful in foraging (Biesmeijer et al. 1998; Seeley 1995). We started training the bees in the morning and we marked five foragers of *P. droryana* individually with acrylic paint using a combination of colored dots with a toothpick. After marked foragers were able to consistently return to the feeder, we started the experiment.

2.3.1. (I) Do cuticular hydrocarbons and the presence of *T. spinipes* affect foraging in *P. droryana*?

We used 20 *T. spinipes* foragers to extract their CHCs and produce a pool. The CHCs were extracted by putting each forager individualized in a glass vial and using hexane as a solvent (Macron Fine Chemicals, 95% n-hexane) to extract its CHCs. After extraction, the vials were let to dry in a flow chamber. Then, each extract was resuspended in 100 µl of hexane, and then the extracts were transferred to a single vial and mixed together. This pool containing 2000 µl of CHCs was then used in the preference tests as chemical cues. In addition, we collected foragers to use in preference tests as visual cues and they were killed in a freezer to avoid damages to the individual and maintain its physical integrity that was previously washed in hexane in order to remove its CHCs.

The setup of the experiment was the same as the training with a 50% sucrose solution. After five marked *P. droryana* foragers were established on this feeder, it was removed. Then, two feeders with a distance of 12 cm between them were placed at the same location as the previous one (Figure 1). This distance is enough to allow bees to perceive the two feeders, so they can distinguish and use both as different sources of food (Lichtenberg et al. 2011). We performed two different tests, one with only visual cues and the other with only chemical cues. For the chemical cue test, 100 µl of *T. spinipes* extract was dripped onto one of the feeders, while 100 µl of hexane was placed at the other one as a control. In the preference test using visual cues, a dead *T. spinipes* forager that was previously washed in hexane in order to remove its CHCs was placed in a feeder, and 100 µl of hexane was used as a control in another one. A new dead *T. spinipes* was positioned at the feeder in each repetition, simulating resource collection from this individual. The position of the feeders (left/right) was randomized during the preference tests, changing after each trial to avoid bias. Each experiment was independently conducted, with visual and odor cues being used separately in experiments I–II. Each repetition of the test was performed for

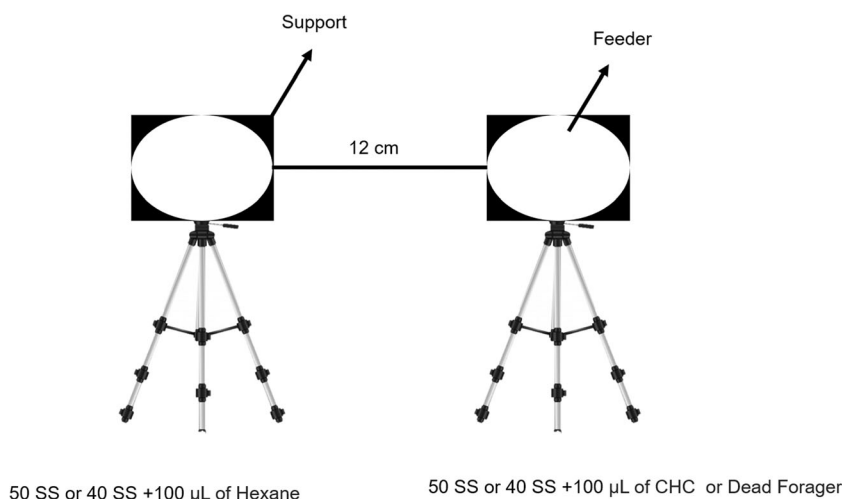


Figure 1. Representation of feeder layout and experimental settings. A camera tripod, a beamed stand, and a glass containing sucrose solution (SS) were used; 100 µl of hexane was used in the control and 100 µl of *Trigona spinipes* cuticular hydrocarbons (CHC) or one dead forager of *T. spinipes* was used.

2 min and was videotaped with two cameras, one for each feeder. Each test was made 15 min apart, and 26 repetitions were performed for each preference test. Between each repetition, the feeder was washed with hexane to remove the applied CHCs, which were subsequently reapplied before each new test. We also changed the sucrose solution between each repetition. The number of visits was counted during video analysis and the criteria adopted for visitors were foragers that collected resources (foragers that everted their proboscis and drank the solution).

2.3.2. (II) Does the presence of *T. spinipes* at a low sugar feeder affect foraging activity in *P. droryana*?

A preference test was performed with the same spatial configuration as the first experiment, but the sugar concentration used was 40% instead of 50% (the value received from food sources), so we tested whether a lower sugar concentration could influence the foraging behavior of *P. droryana*. One hundred microliters of hexane was used as a control in one feeder and a dead *T. spinipes* forager was placed at the other one. We used the same recording setup as the first experiment and we also counted the number of visits at each feeder, as previously defined. We

did not perform the same test with CHCs, as in experiment I; due to the abrupt death of all the *P. droryana* the focal colonies before the tests could begin.

2.4. Statistical analysis

The preference tests from experiments I and II were individually analyzed via the *G* test of goodness-of-fit, with an expected ratio of 50% for each number of observations in each category. In both experiments, we utilized the number of visitors at each food source as the observed number. Since our focus was the number of visitors at the feeder, it is possible that the same individual was counted more than once in all of the experiments.

All data were analyzed in R version 3.6.2 (R Core Team 2019). We utilized the package RVAideMemoire (Hervé 2020) for the *G* test. All graphics were plotted using the package ggplot2 (Wickham 2016).

3. RESULTS

We identified 26 CHCs from the chromatogram pool samples regarding *T. spinipes* footprints. These chemical compounds ranged from 23 to 33 of carbon chain lengths. Two types of the chemical class were found, being linear alkanes

and unsaturated alkenes; overall linear alkanes were more abundant (Table I).

3.1. (I) Do cuticular hydrocarbons and the presence of *T spinipes* affect foraging in *P. droryana* ?

The feeder containing *T. spinipes*’ CHCs was visited by 75 visitors (51%), while the control feeder was visited by 73 visitors (49%). There was no statistical difference between them (*G* test, *G*=0.027, *df*=1, *p*=0.86) (Figure 2). When using

a dead *T. spinipes* at the feeder, it was visited by 133 visitors (47%), and the control received 153 visits (53%). Once again, groups were not statistically significant different from each other (*G* test, *G*=1.399, *df*=1, *p*=0.23) (Figure 3).

3.2. (II) Does the presence of *T. spinipes* at a low sugar feeder affect foraging activity in *P. droryana* ?

The number of foragers visiting the feeder that contained a dead specimen of *T. spinipes* was 161

Table I. *Trigona spinipes* cuticular compounds identified in the chromatogram pool sample *n* = 5 individuals. Retention time (time in minutes); retention index (R. index). Diagnostic/molecular ions represent the ions we found in the mass spectrum of each peak in the chromatogram that allow us to identify the CHC identity. % area represents the percentual of each peak found in the chromatogram based on the pool of five bees

#	Identity of compound	R. time	R. index	Diagnostic/molecular ions	Pool <i>n</i> = 5 individuals - % area
1	Heneicosene	23.150	2047	294	0.710
2	Heneicosane	23.195	2100	296	1.320
3	Docosane	24.131	2200	310	1.410
4	Tricosane	25.035	2300	324	3.270
5	Tetracosane	25.902	2400	338	4.260
6	Pentacosene - 1	26.533	2475	350	0.400
7	Pentacosene - 2	26.572	2480	350	0.830
8	Pentacosane	26.739	2500	352	11.340
9	Hexacosane	27.536	2600	366	8.990
10	Heptacosene - 1	28.128	2676	378	0.340
11	Heptacosene - 2	28.180	2682	378	0.430
12	Heptacosane	28.313	2700	380	19.940
13	Octacosene	28.994	2792	392	0.750
14	Octacosane	29.052	2800	394	9.060
15	Nonacosene - 1	29.584	2873	406	0.270
16	Nonacosene - 2	29.615	2878	406	0.510
17	Nonacosane	29.773	2900	408	14.960
18	triacontane	30.462	3000	422	6.490
19	Hentriacontene - 1	30.881	3062	434	0.470
20	Hentriacontene - 2	30.961	3073	434	0.320
21	Hentriacontene - 3	31.001	3079	434	0.380
22	Hentriacontane	31.137	3100	436	6.920
23	Unknown	31.663	3173	-	0.330
24	Dotriacontane	31.848	3200	450	3.440
25	Tritriacontane	32.638	3300	464	2.150
26	Pentatriacontane	34.570	3500	492	0.710

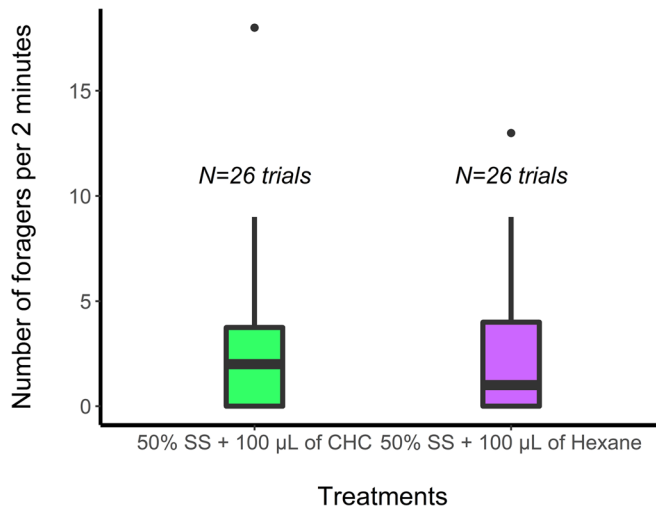


Figure 2 The effect of cuticular hydrocarbons (CHCs) of the aggressive bee. The average number of bees visiting the 50% sucrose solution (SS) feeders, with and without 100 µl of *Trigona spinipes* cuticular hydrocarbons (CHCs), over a period of 2 min. The horizontal bars of the boxplots indicate the medians and boxes delimiting the first and third quartiles; circles are outliers.

(29%), while the control feeder was visited by 387 visitors (71%). There was a statistically significant difference in the number of visits between the feeders, with bees displaying a negative reaction to the one containing the dead *T. spinipes* specimen (G test, $G=96.04$, $df=1$, $p<0.001$) (Figure 4).

4. DISCUSSION

Our results of experiment I suggest that the *T. spinipes* CHCs on the artificial feeders did not affect the foraging activity of *P. droryana* foragers in the sugar concentration tested in our study. Compared with the control, the 50%

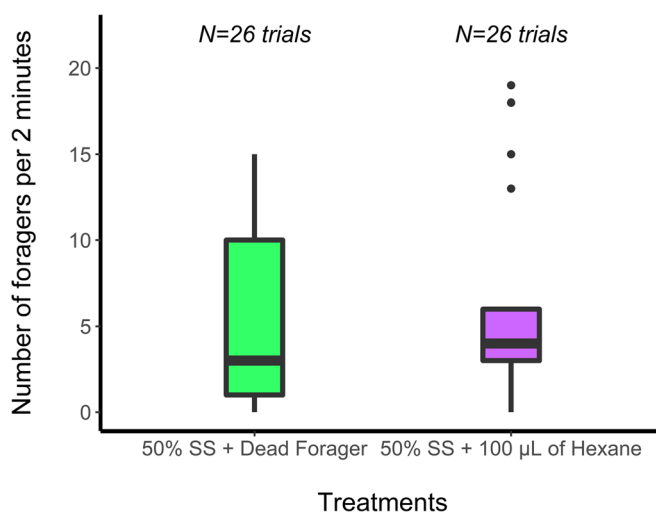


Figure 3. The effect of the presence of aggressive bee. The mean number of bees visiting the 50% sucrose solution (SS) feeders, with and without a dead forager of *Trigona spinipes*, over a period of 2 min. The horizontal bars of the boxplots indicate the medians and boxes delimiting the first and third quartiles; circles are outliers.

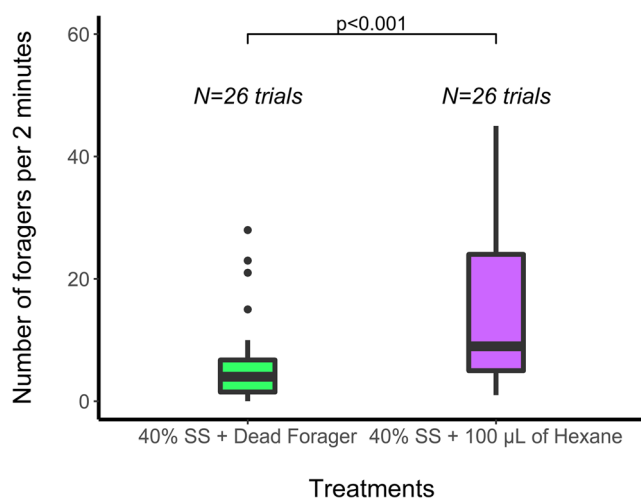


Figure 4. The effect of sugar concentration. The mean number of bees visiting the 40% sucrose solution (SS) feeders, with and without a dead forager of *Trigona spinipes*, over a period of 2 min. The horizontal bars of the boxplots indicate the medians and boxes delimiting the first and third quartiles; circles are outliers.

sucrose solution containing CHCs in the support did not change the number of foragers' visits to the food source or its persistence. It can be argued that *P. droryana* foragers use other parameters, to direct its foraging efforts, e.g., the distance of foraging (distance between the nest and the food source), food availability (amount of food available at flower patches), or the rate of which the solution flows at the food source (Macarthur and Pianka 1966; Núñez 1970; Aguilar and Briceño 2002). However, *P. droryana* is an opportunistic species, and since it is offered a highly available sugar-rich food source, perceiving or not the CHCs of *T. spinipes* in the feeder, did not interfere in its foraging activity. In addition to that, the feeder was positioned 5 m away from the colony, thus providing a high cost-benefit ratio to the foragers, since they would spend less energy to collect resources in comparison to a more distant food source (Heinrich and Raiven 1975). Thus, *P. droryana* foragers did not respond negatively to these CHCs or, if they are able to perceive, they ignored these cues, since the resource with high sugar concentration and its location (close to the colony) provide a greater benefit than a possible attack by an aggressive species. This could explain why CHCs did not affect the number of visits between treatments.

In the experiment with dead individuals of *T. spinipes* at the 50% sugar solution feeder,

although we did not observe a significant difference in the number of visits, *P. droryana* foragers seemed to discriminate the presence of the aggressive species. For example, they performed some behaviors, such as an approximation (approaching the individual but not touching it), observation (being around the individual from distance), and attacking (touching or biting the individual). Since they received no aggressive act, they continued to collect resources normally (personal observations), which can suggest that the presence of the dead individual did not affect their foraging activity in this sugar concentration. It is possible that we would obtain different results if using an alive *T. spinipes*, that could move and respond to these behaviors displayed by *P. droryana* foragers, since the cost of foraging would certainly increase due to attacks from the aggressive species. Therefore, the presence of dead foragers from an aggressive species with a 50% sugar solution did not cause an avoidance behavior at the food source. However, none of the three foraging behaviors previously mentioned were found with the experiment using 40% sugar concentration and dead *T. spinipes* foragers (visual cues). In other words, *P. droryana* foragers did not show aggressive behavior towards *T. spinipes* possibly due to the relatively low sugar concentration at the feeder, since they are able to discriminate it via odor (Han et al. 2010). Even if they can identify *T. spinipes*

as an aggressive species, it is a possibility that this sugar concentration did not prove to be advantageous at a cost-benefit ratio to incite a direct confrontation against this competitor. Thus, the presence of foragers of an aggressive species influenced the behavior of food source avoidance (local inhibition in a lower sugar concentration food source) (Parrish and Fowler 1983; Richter and Tisch 1999).

Bees of the genus *Trigona* tend to forage in food sources containing high sugar concentrations with great availability of food and commonly recruit nestmates by depositing pheromones directly at the source or as a trail between it and the nest (Hölldobler and Wilson 1990; Nieh 2004). Since *P. droryana* is known to be an opportunistic and persistent species at food sources (Biesmeijer et al. 1998; Seeley 1995), it may have developed a strategy throughout evolution to be able to identify chemical or visual cues left by its competitors. Moreover, a possibility is that the CHCs which are derived from a bee that explores food sources with high availability and profitability could be considered a local enhancement (the attraction caused by a food source that is occupied by other foragers; Thorpe 1956; Slaa et al. 2003). This foraging strategy was mainly studied in vertebrates and it seems to be the most important mechanism for social foraging (Galef Jr and Giraldeau 2001). Thus, the role of local enhancement in foraging can have two functions: (1) to facilitate the discovery of new food sources and (2) to facilitate the formation of foraging groups (Beauchamp et al. 1997). Thus, in species that recruit nestmates, local enhancement leads to the formation of dense foraging groups, which may be an advantage for the defense of the food source against other individuals, especially aggressive ones. However, the role of local enhancement in species that do not recruit nestmates, which is probably the case of *P. droryana*, is not well understood, as local enhancement is unlikely to lead to the formation of dense foraging groups in the absence of recruitment. However, *P. droryana* is an opportunistic species and since it is offered a highly available sugar-rich food source, perceiving or not the CHCs of *T. spinipes* in the feeder, did not interfere with its foraging activity. In addition, the feeder was

positioned 5 m away from the colony, thus providing a high cost-benefit ratio to the foragers, since they would spend less energy to collect resources in comparison to a more distant food source (Heinrich and Raiven 1975).

There are records of both species visiting two flower species (Pansarin and Amaral 2006), with *P. droryana* even outnumbering *T. spinipes* in one species during the observed time. This fact coupled with the opportunistic and solitary foraging style of *P. droryana* can be used to infer that this species may be able to access the information of its competitors and exploit an advantageous food source at a low cost/benefit ratio. It is possible that this foraging behavior displayed is controlled by the cost/benefit ratio of spending more energy scouting for an advantageous food source or utilizing its competitors' cues to their advantage at the risk of facing a confrontation. Our results regarding experiment II help to support this hypothesis, because when they were faced with a relatively lower sugar concentration, the foragers avoided the feeder containing the visual cue and chose the other one instead, even if it was close to the nest entrance. The order of the presentation may also have influenced the outcome of the experiment. The control feeder was presented first, followed by the one containing the visual cues and CHCs one lastly. Although it is just a possibility, the fact that the number of foragers increased in this order adds to both the hypothesis of local enhancement and that they learned the location of the feeder and started visiting in greater numbers as the time passed, since the feeder was always placed at the same position and distance from the colony. More studies are required to infer which of these possibilities are more inclined to influence their foraging behavior.

Our results corroborate with the optimal foraging theory, as *P. droryana* foragers exploited more advantageous resources (50% sugar solution), even if it contained cues of aggressive species on it. The energy cost during the foraging seems to be important, due to the avoidance displayed by foragers at the feeder containing 40% sugar solution when faced with the visual cues of *T. spinipes*. The cost of possibly encountering a competitor and entering in the confrontation was not worth it considering the lower sucrose percentage and subsequently lower energy intake.

Considering our results, our hypothesis is that there is evidence of a probable increase of risk tolerance with increased resource reward (sucrose solution), and that visual cues play an important role on decision making of foraging, but the additional cues that were not observed in this study may also be important, such as response behavior of an aggressive competitor following a probing behavior by *P. droryana*. Therefore, these are factors that can determine if *P. droryana* will decide whether a food source is worth exploring or not. It is possible that this species is able to access the risks against the rewards of foraging when it comes across a competitor or a trail left by it. Even under the risk of a direct confrontation, the energy input from exploiting a rich resource is necessary to make it worthwhile. Additional studies are necessary to understand the interactions between chemical and visual cues from competitors, besides testing chemical cues at lower sucrose concentrations. This study was important to better understand the foraging strategy of *P. droryana*, which is still not very well documented, and to access its strategy in terms of risks and rewards regarding the optimal foraging theory. In addition, it contributed to the identification of *T. spinipes* foragers CHCs, which also are not well studied in the literature.

SUPPLEMENTARY INFORMATION

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Availability of data and material All data analyzed during this study were included as a supplementary material.

Code availability Not applicable

AUTHOR CONTRIBUTIONS

JP and FSN planned, designed, and executed experimental work; BG and RCS conducted data analyses; JP wrote the manuscript; and FSN, BG, RCS reviewed the manuscript.

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DECLARATIONS

Ethics approval Not applicable

Competing interests The authors declare no competing interests.

Quand est-il nécessaire d'éviter ses ennemis? Une abeille sans dard ignore les signaux de ses concurrents agressifs pour explorer les sources de nourriture.

stimuli chimiques / abeilles sans dard / stratégie de recherche de nourriture / empreinte.

Wann ist es notwendig, sich vor deinen Feinden zu schützen? Eine stachellose Biene ignoriert aggressives Verhalten von Rivalen bei der Futtersuche.

Chemische Reize / stachellose Bienen / Sammelstrategie / Fußabdruck.

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