

Article

Honey Bee Foraging Decisions Influenced by Pear Volatiles

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Abstract: The interactions between plants and pollinators are complex. Flower volatiles as special olfactory cues could influence the foraging choices of pollinators. Here, we conducted bioassays to evaluate the role of flower volatiles on the attraction of honey bees (native *Apis cerana* and exotic *Apis mellifera*) to pears (native *Pyrus bretschneideri* and exotic *Pyrus communis*). Chemical and electrophysiological approaches were used to determine flower volatiles and evaluate the antennal responses of honey bees to volatiles from pear flowers. Bioassays demonstrated that flower volatiles were crucial for the attraction of honey bees to pear flowers; honey bees preferred to forage on *P. communis* flowers ($p > 0.05$), with approximately $64.37 \pm 0.02\%$ (*A. mellifera*) and $62.10 \pm 0.02\%$ (*A. cerana*) foraging on *P. communis*. Flowers of *P. communis* and *P. bretschneideri* yielded 27 and 31 compounds, respectively, with 17 of them being common. Honey bee antennae responded to 16 chemicals, including 5 contained in both pear species: 1-nonanol, linalool, methyl 2-hydroxy-3-methylpentanoate, methyl L-isoleucinate, and α -farnesene. In addition, there were 8 electrophysiologically active compounds in *P. bretschneideri*: methyl L-valine ester, benzaldehyde, 6-methyl-5-hepten-2-one, isophorone, 2-methyl octane, longicyclene, longifolene, and caryophyllene; and 3 electrophysiologically active compounds in *P. communis*: β -ocimene, 4-oxoisophorone and lilac alcohol D. In conclusion, our study demonstrated the significant impact of pear flower volatiles on honey bee foraging choices. This knowledge provides a basis for the selection of honey bees for pear pollination and lays a foundation for further study of the chemical communication of pear attractiveness to honey bees.

Keywords: pear; honey bee; foraging behavior; flower volatiles; GC-MS; GC-EAD



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1. Introduction

Approximately 90% of flowering plants worldwide rely on interactions with various pollinators in their environments for reproduction, and insects account for the majority of pollinators and perform pollination services for approximately 75% of global crops [1,2]. The long period of coevolution between pollinators and flowering plants has led to a complicated and mutually beneficial pollinator–plant relationship. Plants evolved direct and indirect floral traits, such as color, floral scent, and flower rewards (pollen and nectar), to attract pollinators by visual or olfactory signals [3]. Bees are capable of learning floral signals during their foraging bouts [4–7]. Nevertheless, insufficient, or inefficient pollination is still common in several crops and is caused by the foraging bias of pollinators [8,9]. Knowledge about the foraging decisions of pollinators on crops is still scarce [10,11].

Pear is an insufficiently and inefficiently pollinated crop. Due to their self-incompatibility, pear plants are highly dependent on insects or artificial pollination [12,13]. Among insect pollinators, bees, including honey bees, bumble bees, and solitary bees, are the pollinators

with the greatest potential for pear pollination [14–16]. Honey bees are commonly regarded as the primary pollinators. However, it was demonstrated that pear flowers are not as attractive as the flowers of other crops, such as apple, peach, and rape, due to the low volume and sugar concentration of their nectar [13,14,17]. Microorganism inoculation, bee attractants, pollen trapping, and syrup feeding have been explored to promote honey bee foraging and pear pollination in orchards [18–20].

Studies have chemically characterized the floral scent of pear and identified those compounds thereof that are physiologically active in honey bees [21,22]. Linalool + methyl benzoate or methyl 2-hydroxy-3-methylpentanoate were the most abundant compounds in several European pear cultivars (*P. communis*), and 17 were electrophysiologically active in honey bee antennae [22]. For native pear species, 3-methyl-1-butanol and (+)-limonene volatiles were thought to have the highest relative content, and 6-methyl-5-hepten-2-one, 2-phenethyl alcohol, and 1-nonanal showed low attraction to honey bees [21]. To date, no study has compared the scent of these two pear species, and there might be differences in their floral scents, with a potential impact on attractiveness to pollinators.

China contains the most plentiful *Pyrus* germplasm resources in the world and is the world's leading country in pear production [23]. *Pyrus bretschneideri* (Rosales: Rosaceae) is the most important commercial and endemic pear species and comprises approximately 23% of the total pear production in China [24]. *Pyrus communis* (Rosales: Rosaceae) is a common European pear species that has been cultivated in parts of China in recent years [25]. Both pear species rely on honey bee pollination for successful fruit sets. Two managed honey bee species, *A. cerana* and *A. mellifera*, are the most promising honey bees for pear pollination in China. *Apis cerana* is an endemic bee species in Asia and is an important pollinator of native plants [26]. *Apis mellifera* is the most popular bee species reared around the world and is the most important pollinator for crops [27,28]. Both honey bees were mass reared and have been demonstrated to be the main pollinators of pear in China [16]. In particular, about 50% of pears in production at present are artificially pollinated, which has many disadvantages such as large labor and high cost [29]. It is essential to explore the foraging decision of both honey bees on pears to replace hand pollination.

Honey bees play an important role in the pollination of pear, yet the foraging choices and olfactory cues honeybees use when foraging on pear flowers are unknown. The foraging behaviors of native *A. cerana* and exotic *A. mellifera* on native pear *P. bretschneideri* and exotic pear *P. communis* were studied, and the biological activity of the pear flower volatiles in antennae of honeybee pollinators was studied by using gas chromatography-mass spectrometry (GC-MS) and gas chromatography coupled to electroantennographic detection (GC-EAD). The following questions were addressed: (1) Do native honey bees prefer to forage on native pear species? (2) Does pear species affect honey bee foraging decisions? (3) Do the antennae of honey bees respond to the compounds released by pear flowers? The results from this study will help to guide efforts to support pear pollination.

2. Materials and Methods

2.1. Pear Orchard and Honey Bees

This study was conducted in a pear orchard in the Yuncheng region, Shanxi Province, China. The area of the pear orchard was approximately 6.6 hectares. *Pyrus bretschneideri* is the dominant species planted in the orchard. The distance between rows was 3.5 m, and the distance between adjacent trees within a row was 3 m. The pear trees were approximately 20 years old. A few *P. communis* trees were planted to test their adaptability on the side of the orchard. Both pear species were cared for according to professional management suggestions.

At least six colonies of each honeybee *A. cerana* and *A. mellifera* was prepared every year. All colonies (never having foraged on pears before) were in single Langstroth hives and adjusted to equal honeybee populations (approximately 3000–3500 workers), each with two frames. Each colony had a laying queen, a few larvae, and little pollen and nectar.

Bees were introduced to a flight cage one day prior to observation to acclimatize to the cage environment.

2.2. Behavioral Observation Experiment

2.2.1. The Flight Cage Arrangement

The experiments were performed in flight cages (6 m × 4 m × 3 m), which consisted of a steel frame covered with a fine nylon mesh (20 mesh) (Figure 1A). Two flight cages were built in an open, flat area of the orchard, about the center of the orchard surrounding by pear trees, and adjacent to each other to ensure that the climate factors inside the cages were similar. Clean water was supplied in plastic basins. Four to five newly blossoming *P. bretschneideri* and *P. communis* twigs with approximately 30 flowers containing anthers carrying pollen for each pear species were cut from trees and placed on a well-watered clay flower board (Figure 1B). The two flight cages were with both pear species, and each cage was for one honeybee species (one for *A. mellifera* and the other for *A. cerana*). The flowers were replaced by new pear flowers when the anthers were empty. The clay flower boards were watered every hour to maintain moisture.

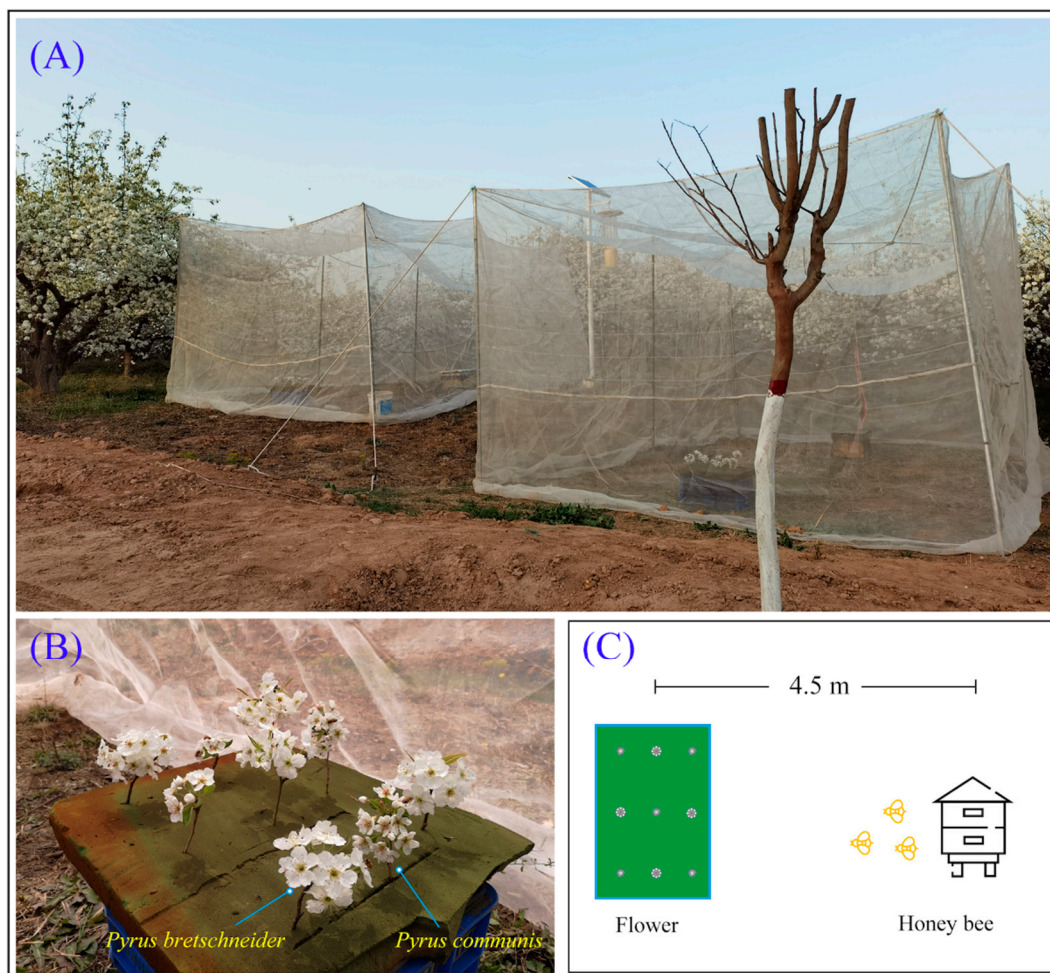


Figure 1. Behavioral observation experiment. (A) Flight cages; (B) flowers of *P. bretschneideri* and *P. communis*; (C) schematic setup of pear flowers and honey bees in the flight cages.

2.2.2. Behavioral Observation

The relative attractiveness of *P. bretschneideri* and *P. communis* pear flowers to honey bees was determined during the peak pear flowering period from 2019 to 2021. Pear flowers were placed 4.5 m from the hive (Figure 1C). Observations were conducted from 9:00 a.m. to 17:00 p.m., and each observation lasted for 10 min per hour. The number of honey bees

landing on flowers to gather pollen or nectar was recorded. Daily records were used for statistical analysis. The positions of the flowers from the two pear species were changed daily to avoid the potential influence of location memories during honey bee foraging. Meteorological data such as daily temperature and relative humidity were recorded. The experienced observers were rotated daily to prevent observer bias. Since the pear flower blooming period lasted only a few days, we replicated the experiment over 3 years to have enough data and repetition for statistical power.

2.3. Flower Volatile Collection

To determine the extent to which pear flower volatiles influence honey bee foraging preferences, we collected volatile samples from *P. bretschneideri* and *P. communis* flowers in situ from 10:00 a.m. to 4:00 p.m. during the blooming period. One *P. bretschneideri* and one *P. communis* flower twig in full bloom were randomly selected and bagged with Tedlar PVF bags (1 L). Quartz glass tubes (length: 120 mm; inner diameter: 6 mm) filled with 150 mg Tenax-TA (mesh 60–80, Supelco, Bellefonte, PA, USA) were connected with an atmospheric sampler (QC-2B, BMILP Science & Technology Development, Beijing, China) by Teflon tubes, and the volatiles emitted from the flowers were trapped in the absorbent tubes. The flow rate was adjusted to 500 mL/min by a flowmeter, and samples were collected for 2.5 h. Samples were also collected from empty bags as controls. The trapped volatiles were eluted with 2 mL n-hexane (Sigma-Aldrich, St. Louis, MO, USA), concentrated to 400 µL under a gentle stream of N₂, and stored at −80 °C until use.

2.4. Y-Tube Olfactometer Bioassays

The Y-tube olfactometer (stem 20 cm, arms 15 cm, at an angle of 45°, internal diameter of 2.2 cm) was used for the bioassays. The olfactometer arms were connected to glass gas desiccators. Ten microliters of volatile samples (*P. bretschneideri* and *P. communis*) were applied to two filter paper strips (3 × 1.5 cm²) and then put into two glass gas desiccators. The paper strips were allowed to evaporate for 30 s before gas was passed from both arms to the stem through cleaned and humidified airflow created by an air pump system with an activated charcoal filter and distilled water. The airflow through each of the olfactometer arms was 500 mL/min. We hung a white fluorescent light directly above the olfactometer to avoid the effect of honey bee phototaxis on selection.

The experimental bee colonies were never exposed to pear flowers. The honey bee foragers (collected from the entrances of the beehives) were tested independently through 5 min observation periods in the olfactometer, and their behaviors were assigned to one of three choices: (1) the individual moved toward the *P. bretschneideri* flower volatile samples (the workers went 5 cm past the Y junction and stayed there for more than 30 s); (2) the individual moved toward the *P. communis* flower volatile samples; and (3) the individual made no choice (the worker did not reach the decision line within 5 min). For each honey bee species, we repeated this test with 50 foragers and compared the number of different choices (i.e., moving toward one of the two pear flower volatile samples).

2.5. GC–MS and GC–EAD

The flower volatile samples of pear were analyzed by GC–MS (QP2010, Shimadzu, Kyoto, Japan) equipped with an HP-5MS column (30 m × 0.25 mm × 0.25 µm, Supelco). Samples were run in a splitless system, and helium was used as the carrier gas (flow: 1.5 mL min^{−1}). One microliter was injected into a 250 °C injector. The GC oven temperature started at 50 °C and was then increased by 10 °C/min to 280 °C, where it was held for 5 min. The MS interface worked at 250 °C. Mass spectra were taken at 70 eV (in EI mode) from 34 *m/z* to 550 *m/z*. Compounds were identified by comparing mass spectra against synthetic standards and NIST 14 library matches. The relative quantity of each compound was calculated by the area of each peak divided by the total area of all compounds.

Gas chromatography coupled to electroantennographic detection (GC–EAD) was used to identify volatile compounds of pear flowers perceived by antennae of *A. mellifera* and

A. cerana workers. The GC–EAD system consisted of a gas chromatograph (Agilent 7890A, Santa Clara, CA, USA) equipped with a flame ionization detector (FID) and an EAD setup provided by Syntech (Kirchzarten, Germany). A 3 µL aliquot of each scent sample was injected (temperature of injector: 250 °C) at 50 °C oven temperature, and the GC program was the same as GC–MS. In the electrophysiological experiments, flower volatiles of *P. communis* were tested on the antennae of 12 *A. mellifera* workers and 9 *A. cerana* workers, and flower volatiles of *P. breitschneideri* were tested on antennae of 10 *A. mellifera* workers and 10 *A. cerana* workers.

The bees were caught at the entrance of hives, and antennae were cut off with iris scissors under the microscope, mounted between two glass capillary electrodes that were filled with Ringer’s solution (8.0 g/L NaCl, 0.4 g/L KCl, 0.4 g/L CaCl₂), and connected to silver wire electrodes. The reference electrode was in contact with the cut surface of an antenna, while the recording electrode was in contact with the cut tip of an antenna. A flower volatile compound was described as EAD-active when it elicited an antenna response in at least half of the replicates. All EAD-active compounds were identified by GC–MS.

2.6. Data Statistics

The chi-square goodness of fit test was applied to daily field observation data and Y-tube test results to determine the foraging preference of bees between pear flowers. The number of bees observed every 10 min of the day was added up as daily observation data. The null hypothesis in these tests was that honey bees were equally attracted to the *P. communis* and *P. breitschneideri* pear flowers. Individual honey bees who did not respond to the Y-tube olfactometer were omitted from the statistical analysis. A generalized linear model (GLM) was used to examine the foraging proportion for differences in foraging between bee species on each pear species. The foraging proportion is the ratio of the number of bees that visited each pear species on a given day to the overall number of bees on that day. The observational data were separated into three groups by year, as observations were conducted in various years. The GLM included ‘honey bee species’ and ‘pear species’ as fixed factors, and ‘year’ as the random factor. The relative contents of flower volatile components of two pear species were calculated from the ratio of the peak area of each compound to the total peak area.

3. Results

3.1. Foraging Choices of Honey Bees on Pears

The three-year flight cage experiments showed that both honey bee species significantly preferred *P. communis* flowers over *P. breitschneideri* flowers ($p < 0.01$). On the first day of the experiment each year, there was little preference for honey bees foraging choices, and a low number of bees were recorded foraging on pear flowers (Figure 2).

Eleven days of observation showed that the number of *A. cerana* individuals foraging on *P. communis* was significantly higher than that foraging on *P. breitschneideri* ($p < 0.01$, Figure 2A). The numbers of *A. cerana* foraging on pear flowers daily ranged from 70 to 1181. The maximum number of *A. cerana* observed foraging on *P. communis* was 781, while 400 *A. cerana* individuals were foraging on *P. breitschneideri* ($\chi^2 = 122.914$, $p < 0.001$). The minimum number of *A. cerana* observed foraging on *P. communis* was 54 bees, and on *P. breitschneideri*, it was 16 bees ($\chi^2 = 20.629$, $p < 0.001$) (Figure 2A).

The foraging preferences of *A. mellifera* differed significantly between *P. communis* and *P. breitschneideri* flowers ($p < 0.05$, Figure 2B). The numbers of *A. mellifera* foraging on pear flowers daily ranged from 41 to 248 bees. The maximum number of *A. mellifera* foraging on *P. communis* was 149, while that on *P. breitschneideri* was 99 bees ($\chi^2 = 10.081$, $df = 1$, $p < 0.001$). The minimum numbers of *A. mellifera* foraging on *P. communis* and *P. breitschneideri* were 27 and 14 bees ($\chi^2 = 4.122$, $df = 1$, $p = 0.042$), respectively.

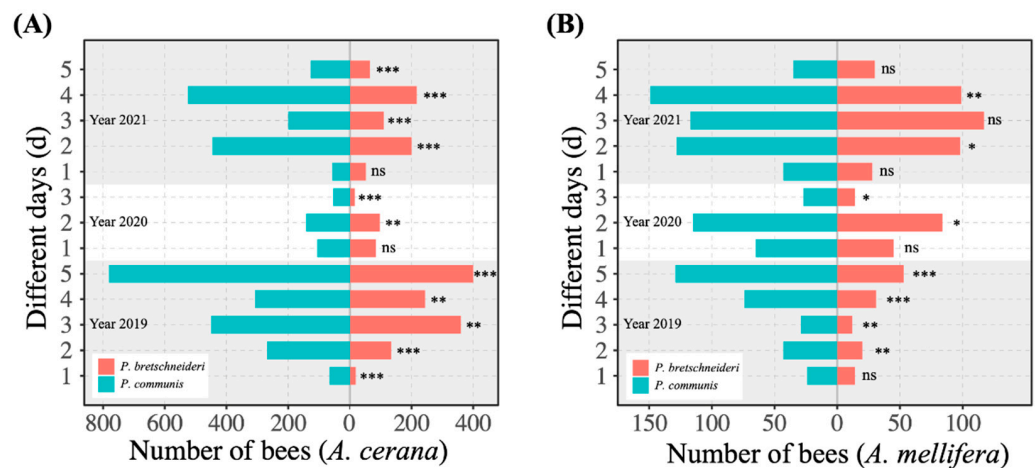


Figure 2. The daily foraging choices of honey bees. (A) Choices of *A. cerana*; (B) choices of *A. mellifera* (ns: $p > 0.05$; *: $0.01 < p < 0.05$; **: $0.001 < p < 0.01$, and ***: $p < 0.001$).

3.2. Comparison of the Proportion of Honey Bees Foraging

Foraging proportions were significantly affected by pear species, whereas bee species and year had no effects (generalized linear model, bee species: $p = 0.26$; pear cultivar: $p < 0.001$ and year: $p = 1.00$). The exact differences between bee species are shown in Table 1. The foraging proportion in *P. communis* was higher for both *A. cerana* and *A. mellifera* than in *P. bretschneideri* (Figure 3).

Table 1. Generalized linear model (calculated Wald χ^2 and p value) of the effect of bee species (*A. cerana* and *A. mellifera*), pear species (*P. bretschneideri* and *P. communis*) and year on single pear flower foraging proportion.

Bee Species	Factors	Foraging Proportion	
		Wald χ^2	p -Value
<i>Apis cerana</i> and <i>Apis mellifera</i>	Bee species	3.2411×10^{-29}	0.260
	Pear species	175.67	<0.001
	Year	2.287×10^{-28}	1.000

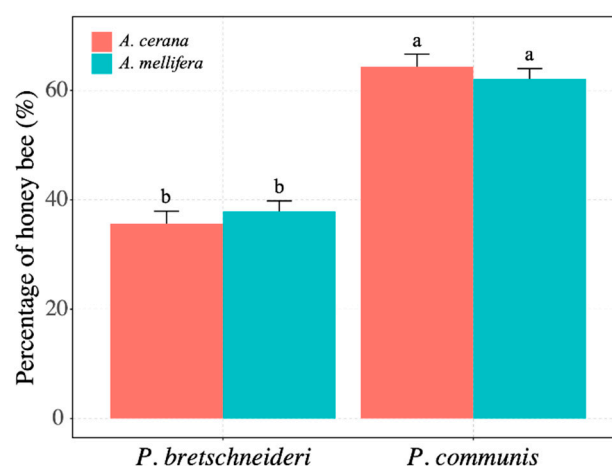


Figure 3. The mean proportions of *A. cerana* and *A. mellifera* foraging on *P. communis* and *P. bretschneideri* (mean $\pm$ SE; $n = 13$ for both bee species). Different letters indicate a significant difference ($p < 0.05$).

The proportions of *A. cerana* and *A. mellifera* that foraged on *P. bretschneideri* were $35.63 \pm 0.02\%$ and $37.90 \pm 0.02\%$ ($p > 0.05$), respectively. For *P. communis*, *A. mellifera* showed a weaker preference than *A. cerana* at $64.37 \pm 0.02\%$ and $62.10 \pm 0.02\%$ ($p > 0.05$), respectively,

according to records over three years. Both *A. cerana* and *A. mellifera* visited more *P. communis* flowers per year than *P. bretschneideri* flowers, with a similar foraging proportion.

3.3. Y-Tube Olfactometer Experiment

The results of the Y-tube olfactometer experiment showed that the honey bee species were significantly affected by pear volatiles ($p < 0.05$). Both honey bee species preferred the volatiles of *P. communis* over those of *P. bretschneideri*. In the experiment with *A. mellifera*, 30 bees (65.22%) were attracted to *P. communis*, 16 bees (34.78%) were attracted to *P. bretschneideri* ($\chi^2 = 4.261$, $df = 1$, $p = 0.032$), and 4 bees did not make a choice. In the experiment with *A. cerana*, 32 bees (71.11%) were attracted to *P. communis*, 13 bees (28.89%) were attracted to *P. bretschneideri* ($\chi^2 = 8.022$, $df = 1$, $p = 0.005$), and 5 bees did not make a choice (Figure 4).

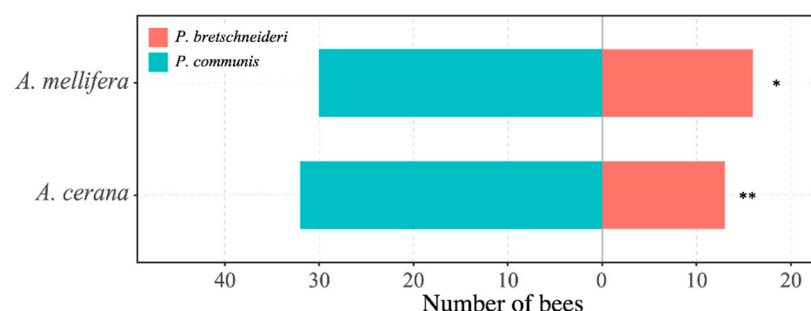


Figure 4. Choices of honey bees regarding different pear flower volatiles according to Y-tube olfactometer tests (*: $0.01 < p < 0.05$, **: $0.001 < p < 0.01$).

3.4. GC–MS and GC–EAD

P. bretschneideri and *P. communis* flowers had considerably different volatile chemicals and relative amounts of those components (Table 2). In total, seven kinds were assigned to 41 compounds that were detected: 9 alkane compounds, 8 alkene compounds, 6 nitrogen-containing compounds, 5 terpenoids, four ketones compounds, three aldehyde compounds, two ester compounds, one alcohol compound, one phenolic compound, and two unknown compounds. Of these 41 compounds, only 17 compounds were detected in both pear species, and the amounts of these compounds also varied between species. Linalool, one of the principal compounds that dominated the fragrances of *P. communis* ($22.92 \pm 9.03\%$) but only accounted for $0.97 \pm 0.78\%$ in *P. bretschneideri*, had a quite striking difference in relative quantity. Methyl L-isoleucinate was the most abundant component in *P. bretschneideri* ($52.60 \pm 2.10\%$) but only $17.95 \pm 3.58\%$ in *P. communis*. There were also variations in other chemicals between species. For example, the content of methyl 2-hydroxy-3-methylpentanoate was $30.68 \pm 3.58\%$ in *P. communis*, whereas in *P. bretschneideri*, it was only $15.25 \pm 3.36\%$.

The antennae of *A. cerana* and *A. mellifera* responded to 16 compounds of all pear flower volatiles (Figure 5). L-valine methyl ester, methyl L-isoleucinate, benzaldehyde, 6-methyl-5-hepten-2-one, β -ocimene, and linalool were the only components that were EAD-active in both bee species. 1-nonanol, methyl 2-hydroxy-3-methylpentanoate, isophorone, 4-oxoisophorone, 2-methyl octane, longifolene, caryophyllene, α -farnesene, and longicyclene were the only EAD-active compounds for *A. cerana*. Lilac alcohol D was the only EAD-active compound for *A. mellifera*. Together, the number of EAD active components in *P. bretschneideri* accounted for 41.94%, while the content accounted for $81.23 \pm 11.08\%$. The number of active compounds in *P. communis* accounted for 29.63%, and their content was $78.18 \pm 17.36\%$ of the total volatile amount.

Table 2. Number and relative peak area (% of total for compound classes and single components) of volatiles detected in flower volatile samples of *P. communis* and *P. bretschneideri* and their electrophysiological activity in antennae of honey bees (antennae responding to a compound).

No.	Volatile Compounds	KRI	Relative Peak Area (%)		Electrophysiological Activity	
			<i>P. communis</i>	<i>P. bretschneideri</i>	<i>A. cerana</i>	<i>A. mellifera</i>
Nitrogen-containing compounds						
1	L-valine, methyl ester	900		7.7 ± 2.575	✓	✓
2	Methyl L-isoleucinate	999	17.949 ± 3.584	52.574 ± 2.073	✓	✓
3	Methyl nicotinate	1054	1.965 ± 0.762			
4	Benzothiazole	1208		0.549 ± 0.045		
5	1-butanamine, N-(2-pyridinylmethylene)-	1401	0.959 ± 0.557			
6	Benzoic acid, 4-ethoxy-, ethyl ester	1448		0.509 ± 0.037		
Aldehyde compounds						
7	Benzaldehyde	982		0.678 ± 0.283	✓	✓
8	Decanal	1204	0.145 ± 0.103	0.422 ± 0.188		
9	Dodecanal	1402		0.266 ± 0.032		
Ketone compounds						
10	6-methyl-5-hepten-2-one	938		1.033 ± 0.316	✓	✓
11	5,9-undecadien-2-one, 6,10-dimethyl-	1420		0.769 ± 0.192		
12	2,6-di-tert-butyl-p-benzoquinone	1633		0.291 ± 0.03		
13	2,5-cyclohexadiene-1,4-dione, 2,5-diphenyl-	2353	0.163 ± 0.129	0.589 ± 0.018		
Alcohol compounds						
14	1-nonanol	1104	0.665 ± 0.47	0.165 ± 0.059	✓	
Ester compounds						
15	Methyl 2-hydroxy-3-methylpentanoate	983	30.675 ± 3.582	15.254 ± 3.358	✓	
16	Tris(1-chloro-2-propyl) phosphate	–	0.272 ± 0.582			
Phenol compounds						
17	Phenol	901	5.188 ± 2.018	4.078 ± 3.545		
Terpenoid compounds						
18	β-ocimene	976	2.005 ± 0.499		✓	✓
19	Linalool	1082	22.917 ± 9.032	0.969 ± 0.786	✓	✓
20	Isophorone	1097		0.414 ± 0.063	✓	
21	4-oxoisophorone	1268	3.502 ± 0.449		✓	
22	Lilac alcohol D	1251	0.224 ± 0.074			✓
Alkane compounds						
23	Octane, 2-methyl	1156		0.261 ± 0.02	✓	
24	Dodecane	1214	0.705 ± 0.504	1.957 ± 0.434		
25	Dodecane, 2,6,11-trimethyl-	1320	0.248 ± 0.024	0.662 ± 0.163		
26	Tridecane	1313		0.361 ± 0.029		
27	Tetradecane	1413	1.504 ± 0.209	3.233 ± 0.009		
28	Hexadecane	1612	1.594 ± 0.344	0.426 ± 0.109		
29	Heptadecane	1711	3.309 ± 0.639			
30	Nonadecane	1653	0.488 ± 0.076	1.15 ± 0.022		
31	Heneicosane	2109	0.892 ± 0.161	0.949 ± 0.127		
Alkene compounds						
32	Longicyclene	1184		0.31 ± 0.079	✓	
33	Longifolene	1398		0.057 ± 0.019	✓	
34	Caryophyllene	1494		0.054 ± 0.007	✓	
35	α-farnesene	1458	0.245 ± 0.121	0.498 ± 0.303	✓	
36	7-hexadecene, (Z)-	1620	0.138 ± 0.008	0.149 ± 0.033		
37	(E,E,E)-3,7,11,15-tetramethylhexadeca-	1940	1.244 ± 0.399			
	1,3,6,10,14-pentaene					
38	9-eicosene, (E)-	2017	1.390 ± 0.286	1.556 ± 0.943		
39	(E)-4,8-dimethylnona-1,3,7-triene	–	1.093 ± 0.767			
Unknowns						
40	Unknown1		0.375 ± 0.08			
41	Unknown2		0.149 ± 0.024	2.122 ± 0.378		

KRI: Kovat's retention index. Bolded numbers and "✓" indicate the compound-elicited honey bee antenna response in at least half of the replicates. "Unknown" means that the compound had not been accurately identified by the NIST library but was present in multiple replicated samples.

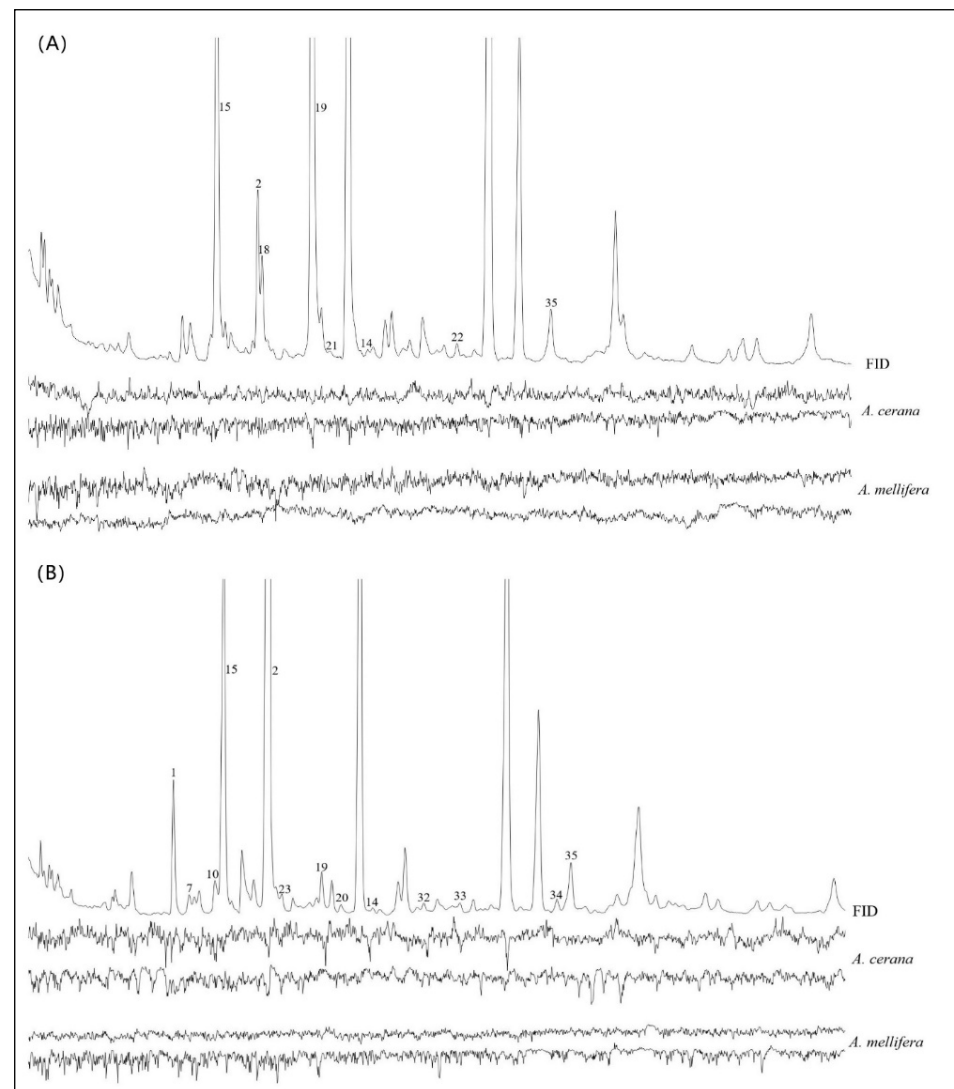


Figure 5. Examples of the antennal responses of honeybee workers (EAD) to volatiles collected from pear flowers (FID). Responses are numbered and correspond to numbers (No.) in Table 2. (A) antennal responses of *A. cerana* and *A. mellifera* workers to volatiles of *P. communis* flowers; (B) antennal responses of *A. cerana* and *A. mellifera* workers to volatiles of *P. bretschneideri* flowers.

4. Discussion

Flowering plants have evolved various floral characteristics to attract pollinators [3]. Flowers have varying degrees of colors, scents, and rewards that contribute to attracting pollinators [1,3]. The findings of this study revealed that pear flower volatiles significantly influence the foraging preferences of honey bees. Both native and exotic honey bees prefer to forage on the European pear *P. communis*. This means that the native honey bees were not prone to foraging on the native pear *P. bretschneideri* when they had a choice. Therefore, the long-term coevolution between the native pear and native honey bee species was less influential than the pear species' identity on foraging behavior. This study offered a foundational understanding of honey bee foraging preference in pear species, which helps influence pear pollination support.

Native plants and pollinators are thought to form a mutually adaptable relationship in the process of coevolution [30]. As an endemic honey bee, *A. cerana* evolved with the native pear species and had a stronger preference than *A. mellifera* for foraging on *P. bretschneideri*, and it has been demonstrated that *A. cerana* has adapted to foraging on less concentrated nectars [16,31]. However, according to the results of the flight cage observations and Y-tube

experiments, *P. bretschneideri* was not more attractive to *A. cerana* than *P. communis* was to *A. mellifera*. This pattern may have been caused by the advantage of the exotic pear, *P. communis*, which has evolved stronger attractive pollination traits, such as the production of volatile compounds, which insects prefer over other traits [22]. No differences were observed in the foraging patterns of either honey bee species on the first day of the field experiment (Figure 2). This pattern may have been caused by the bees that initially touched the pear flowers, causing the foragers to receive negative feedback from the larvae or younger workers feeding on the pollen or nectar [32,33].

Flower rewards have a great influence on the foraging preferences of pollinators. It was observed that the numbers of *A. cerana* and *A. mellifera* foraging on *P. communis* flowers were significantly higher than those foraging on *P. bretschneideri*. The nectar and pollen of pears were demonstrated to be less attractive to bees than those of apples and apricots [13,34]. It was also reported that the foraging activity of honey bees on several Asian pear species differed due to the sucrose contents in nectar, with higher contents increasing the attractiveness of pear flowers [35]. Therefore, the volume and sugar content of nectar are important factors that influence honey bee foraging behaviors [36,37]. The average amount of nectar in *P. bretschneideri* flowers was 1.77 μL /flower, which was lower than that of *P. communis* flowers, which offered a mean volume of 2.8 μL [16,38]. Moreover, the total sugar content of *P. bretschneideri* and *P. communis* were different (64.2 mg/mL and 90 mg/mL, respectively) [16,38]. In addition to nectar, pollen is also a vital food reward that affects the foraging decisions of bees, with the amino acid composition of pollen playing an especially important role [39]. Bees show a preference for pollen that is richer in essential amino acids [13,40]. Low levels of amino acids lead to inferior weight gain, less protein or nitrogen, reduced longevity, and an incomplete development of hypopharyngeal glands (HPG), which could impair the growth of larvae and queens [32,41–44]. The contents of essential amino acids (leucine, valine, and isoleucine) were higher in the pollen of *P. communis* than in that of native pear, *P. bretschneideri* [13,32]. Hence, further study of the influence of the amino acid composition of the pollen from these pear species on honey bee foraging behavior is necessary.

Flower volatiles are considered to be one of the primary determinants of pollinator foraging decisions, especially when flower colors and morphologies are identical [45–47]. The electrophysiological investigations demonstrated that bees are able to perceive volatile molecules from flowers and respond differently to volatile compounds. Honey bees may use flower-specific compounds to locate pear flowers. Of the 108 flower volatiles identified in several European pear cultivars, 17 compounds are electrophysiologically active in honey bee antennae [22]. Among the 76 compounds found in the volatiles of three pear cultivars (Su, Ya, and Xuehua), only 5 compounds generated robust electroantennography (EAG) responses in honey bees [21]. We confirmed that 16 compounds are electrophysiologically active. A few of these compounds, including linalool and 4-oxoisophorone, are known to elicit physiological or even behavioral responses in honeybees [22,48]. These compounds may play a role in the communication between pear flowers and bee pollinators, leading to preference or avoidance responses to various odor stimuli [49]. European pear flower volatiles contain some common floral compounds that have already been identified as being electrophysiologically or behaviorally active in honey bees (linalool, lilac aldehyde, 4-oxoisophorone, etc.) [50–53]. Among all these active compounds, several compounds, such as 6-methyl-5-hepten-2-one, 2-phenethyl alcohol, and 1-nonanal, have been verified to be repellent to bees [21]. The lack of attractive volatile compounds may explain why honey bees are less attracted to honey bees than other contemporaneous flowering plants.

The foraging behavior of honey bees was greatly influenced by pear species, and flower volatiles played a certain role in foraging decisions. The three-year field experiment showed that honey bee foraging was influenced by pear species and their volatiles. The results of the field observation and Y-tube experiments showed that the proportions of the preferences of the two honey bee species were consistent. There were significant differences in the volatiles of *P. bretschneideri* and *P. communis* flowers; several compounds

were physiologically active in honey bees and were potentially behaviorally active. The determination of single volatile compounds in attracting honey bees and the regulatory mechanisms of pear flower volatiles, especially specific odor-related receptor proteins and their functions, are still unclear. It would be interesting to test to what extent the potential functions of the volatiles identified in this study explain the behavior of pollinator switches among species and varieties in orchards.

5. Conclusions

We found that honey bees could make foraging decisions based on pear flower volatiles and had the ability to distinguish specific compounds within them. Our data indicated that bees were able to distinguish European pear *P. communis* from Asian pear *P. bretschneideri* by flower volatiles and had a substantial foraging preference for the European pear *P. communis*, which may be caused by flower volatiles or rewards. The relative contents of principal volatile aroma emissions from two kinds of pear flowers were discovered to be distinct, which led to a difference in the fragrance of the flowers. Furthermore, we discovered that honey bee antennae responded to a number of chemical constituents of flower smell that, depending on their nature or composition, may either attract or repel bees [54]. Despite our investigations of the interactions between honey bees and pears, future research should focus on the precise impacts of certain chemicals on the behavior of honey bees. This study provides a foundation for the combination of pear species in orchards and the selection of honey bees for pear pollination, as well as a foundation for further research into the chemical communication between pears and honey bees.

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