FORAGING BEHAVIOR OF HONEYBEES (*APIS MELLIFERA* L.) AND GROUND BUMBLEBEES (*BOMBUS TERRESTRIS* L.) AND ITS INFLUENCE ON SEED YIELD AND OIL QUALITY OF OIL TREE PEONY CULTIVAR 'FENG DAN' (*PAEONIA OSTII* T. HONG ET J. X. ZHANG)

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Abstract

Oil peony (*Paeonia* spp.) is a new type of woody oil crop in China with a large cultivation area. Inadequate pollination is one of the main reasons for low seed yield. A pollination net room was built at an oil tree peony base, the numbers of honeybees (*Apis mellifera* L.) and ground bumblebees (*Bombus terrestris* L.) were artificially increased and the foraging behaviors and daily activities of the two bees on the plants were observed. Four different pollination methods (honeybee pollination, ground bumblebee pollination, natural field pollination and pollination without insects) were applied. The visit interval, single-flower visit time, number of single-flower visits, number of flowers visited per minute and number of stigma contacts were compared. Meanwhile, the effects of honeybee and bumblebee pollination on the oil yield and quality of peony seeds were compared. There were noticeable differences in daily activity between honeybees and ground bumblebees. Significant differences in the single-flower visit time, visit interval and visit frequency were also observed; honeybee and ground bumblebee pollination increased the seed yield of oil tree peony by 78.74% and 31.88%, respectively. Therefore, both honeybees and ground bumblebees are effective pollinators of oil tree peony. These results provide a theoretical basis for further utilization of bee resources for oil tree peony pollination.

Keywords: foraging behavior, oil peony, oil quality, *Paeonia*, pollination ecology, seed production

INTRODUCTION

Bees are important pollinators of many wild plants and crops and play an important role in maintaining the balance between natural ecosystems and agroecosystems (Xie & An, 2014; Ollerton, 2017; Huang & An, 2018; Toni et al., 2018). According to the Food and Agriculture Organization (FAO), 90% of the food for 146 countries is provided by more than 100 crop varieties, seventy one of which require bee pollination (Klein et al., 2007). Bee pollination directly contributes to crops by increasing

their yield and improving fruit quality (Rader et al., 2012; Fijen et al., 2018). Crop species have different attributes and differ in their degree of dependence on bee pollination (Ollerton, 2017; Toni et al., 2018). Bee pollination of oil crops significantly increase seed yield and oil yield, and cross-pollination can even significantly increase yields for self-compatible crops (Abrol & Shankar, 2012). Honeybees (*Apis mellifera* L.) and bumblebees (*Bombus* spp.), bees with artificially managed colonies, are the most widely used pollinator species in the world and have been widely used to increase

the yield and quality of nuts, fruits, vegetables, oil crops and agricultural crops (Delaplane & Mayer, 2000; Atmowidi et al., 2007; Abrol & Shankar, 2012; Bommarco, Marini, & Vaissière, 2012; Huang & An, 2018). Particularly for large-scale commercial flowering crops that rely on pollinators, honeybees and bumblebees are important colony-forming pollinating bees that alleviate pollination problems (Deguines et al., 2014; Stein et al., 2017). Honeybee pollination increases the seed yield of rape (*Brassica napus* L.) by 18-46% (Sabbahi, DeOliveira, & Marceau, 2005; Bommarco, Marini, & Vaissière, 2012). In sunflower (*Helianthus annuus* L.), the rate of empty shells is reduced and the oil yield of seeds is increased through pollination by honeybees (Said, Inayatullah, & Ali, 2017). Soybean (*Glycine max* L. Merrill) is a self-pollinated oil crop, but pollination by honeybees can increase its yield by 5-20% (Chiari et al., 2005; Abrol & Shankar, 2012).

The tree peony (*Paeonia* spp.), an ornamental flower native to China, is an important medicinal plant and also a high-quality woody oil crop. The oil of its seeds can reach a content over 22% (Li, 2014) and is rich in protein, amino acids and various unsaturated fatty acids; the unsaturated fatty acid content is over 90%, and the α -linolenic acid content in the unsaturated fatty acids may exceed 40% (Li, 2014; Li et al., 2015). The peony is a cross-pollinated plant with a low self-pollination rate and requires pollinators for pollination (Luo et al., 1998; Yang et al., 2015; Zhang et al., 2019). Fengdan (*P. ostii* T. Hong et J. X. Zhang) is the most widely used cultivar of oil tree peony in China. Its flowers are large, with a diameter of 12.5-13 cm, and produce multiple stamens with yellow anthers but no nectarines. The lower and basal parts of the inner surface of the petals are light purplish red, whereas the filaments, stigmas and floral disk are dark purplish red. There are normally five follicles. In mid and late April (spring in China), Fengdan enters the flowering season (Hong et al. 1992; Luo et al., 1998; Hong & Pan 1999). The seeding rate through self-pollination is very low, with an average of only 0.4 seeds per flower (Han et al., 2014; Si, 2016). Although He

et al. (2019) reported that honeybees significantly enhanced the fruit set rate of 'Fengdan', systematic studies on the effect of honeybee pollination on the oil tree peony seed yield are rare. Furthermore, to the best of our knowledge the effect of bumblebees on the seed yield of oil tree peony has not yet been reported.

Based on this information, we conducted systematic research on the foraging behavior of honeybees and bumblebees and their influence on the seed yield and oil quality of oil tree peony. This study was expected to answer the following questions: 1) What are the differences in the foraging behaviors and daily activities of honeybees and bumblebees? 2) Can increasing the number of pollinating bees increase the fruit and seed yields and oil quality of oil tree peony?

MATERIAL AND METHODS

Research Location

The experiment was carried out in 2017 at the peony base (N 34°38'30", E 112°39'43", 125.5 m above sea level) in the East Garden of the Yibin District, which is one of the largest oil tree peony gardens in Luoyang city. The oil tree peony cultivar planted there is 'Fengdan', with an area of more than 106.7 hm². 'Fengdan' peony had entered the fruiting period and was eight years old. More than 3,000 plants were used for this experiment.

Experimental Design

In March 2017, three equally sized pollination net houses were built parallelly in an east-west direction at the oil tree peony base of Luoyang's East Garden. The net houses were 45 m long from east to west, 8 m wide from north to south, 2.1 m in wall height and 3.2 m in ridge height. The nylon mesh was made of a polyethylene material with a hole 1 mm in diameter. Each house was evenly divided into three small net rooms (15 m×8 m×3.2 m). These rooms corresponded to different pollination methods, namely, honeybee pollination (HP), ground bumblebee (*Bombus terrestris* L.) pollination (BP), and a blank control (BC, pollination without insects), with three replicates for each

treatment. Another 45 m×8 m plot was established to the west of the net houses, which included three replicates of the natural field control (FC). The plants in this treatment were pollinated naturally (Fig. 1). For HP, one hive of honeybees was placed in each net room (approximately 6,000 worker bees). For BP, one hive of ground bumblebees was placed in each net room (approximately 80-200 individuals). The honeybees were provided by the Luoyang Lilou Bee Farm, and the ground bumblebees were provided by the Beijing Agricultural Wings Bee Farm.

When the first peony flower in a pollination net room opened, honeybees or ground bumblebees were placed inside. Honeybees were placed in the middle of each net room, 120 cm from the ground. Because there are no nectary glands in peony flowers, a sugar feeder (50% sugar water) was placed in each honeybee and bumblebee hive, and a water feeder (drinking water) was placed near the beehive. The ground bumblebee hives were placed in the middle of each net room, 30 cm from the ground, and a water feeder (drinking water) was placed near

the beehive. The sugar water and drinking water were regularly replenished and replaced.

Observations of Foraging Behavior and Daily Activities of the Bees

To better understand the living habits of honeybees and ground bumblebees for possible application in crop pollination in the future, their foraging behaviors and daily activities were observed.

Foraging Behavior Observation

Between April 14 and 19, 2019, when oil tree peony entered the peak flowering period, the flower visiting behaviors of the bees were observed. Using a stopwatch, the visit interval, single-flower visit time, number of single-flower visits, number of visited flowers per minute and number of stigma contacts by honeybees and ground bumblebees were studied (He, Li, & Zhang, 2012).

The foraging behavior parameters were defined as follows. Visit interval refers to the time it takes for a bee to leave the flower and visit the flower again, including the time when the bee

Fig. 1. Pollination net rooms built at the oil tree peony base. A. oil tree peony base; B. the net house for the bee pollination treatment (45 m×8 m), which is equally divided into three net rooms; C. the net house without pollinating insects; D. plane graph of the pollination experiment. FC, natural field control; HP, honeybee pollination; BP, ground bumblebee pollination; BC, blank control (without pollinating insects).

temporarily leaves the flower to carry pollen in the air over the flowers when visiting the same flower and the time from one flower visit to another. Single-flower visit time refers to the total time it takes for a bee that falls on a flower to leave the flower, that is, the sum of the time spent on a single visit and the time spent combing the pollen over the flower when the bee temporarily leaves the flower. The number of single-flower visits refers to the number of visits per flower by bees (He, Li, & Zhang, 2012; He et al., 2019). The number of visited flowers per minute refers to the number of flowers that each bee visited per minute. The stigma contact ratio refers to the percentage of stigma contacts per flower relative to the total number of single-flower visits.

Daily Activity Observation

From April 14 to 16 (three consecutive days) 2019, the daily activities of the honeybees and ground humblebees in the pollination net rooms were separately observed. Due to a large population of the honeybees, it was difficult to accurately count the numbers of bees that left the nest, returned to the nest and returned to the nest with pollen during the peak period of daily activities. According to literature (He et al., 2019), their daily activities were observed based on the number of bees that visited flowers. Specifically, in each of the three net rooms with honeybees, two 2 m×2 m sample plots were established, and thirty flowers in full bloom were labeled in each sample plot. From 6:00 to 19:00, the number of bees that visited the flowers in each plot within 10 min every 30 min was recorded. In the three net rooms with ground bumblebees, the numbers of bees that left the nest, returned to the nest and returned to the nest with pollen within 10 min every 30 min were counted (An et al., 2007). In the meantime, the temperature and relative humidity near the nest entrance of the honeybees and ground bumblebees were recorded during different time intervals with a hand-held meteorological instrument (Kestrel 3000).

Assessment of Pollination Efficiency

In early August, the follicles of oil tree peony were harvested (most of the follicles were a golden color). During a single-fruit harvest, the picked fruit was wrapped in newspaper, the fruit follicles of each plant were placed in a single nylon mesh bag, and the follicles of each net were placed in a single woven mesh bag. In the laboratory, the fruit follicles were placed on a ventilated and transparent balcony and matured for approximately fifteen days. After the follicles naturally cracked, the number of fruits per plant, the number and weight of seeds per follicle, and the number and weight of seeds per plant from the different pollination treatments were determined. Finally, the seed yield under different pollination treatments was calculated.

Peony Seeds and Determination of the Quality of Seed Oil

The kernel percentage of peony seeds was determined by manual peeling, and 100 seeds were taken from each sample. This process was repeated three times.

The oil yield of peony seeds was determined by a supercritical CO₂ extractor (HA220-50-06; Huaan, Nantong, China). The extraction conditions were as follows: extraction II: 40°C, 30 MPa; separation I: 40°C, 10 MPa; separation II: 35°C, 5 MPa; sample volume: 200 g; and sample material: peony kernel powder that passed through a sieve of 20-40 mesh per inch (approximately 0.42-0.84 mm).

The fatty acid content of peony seed oil was determined by gas chromatography (Agilent-7890, USA). The specific method followed GB 5009.168-2016 (2016) in the national food safety standards. Peony seed oil fatty acid content was determined by the Agricultural Products Quality Supervision and Inspection Center (Zhengzhou) of the Ministry of Agriculture.

Statistical Analysis

Statistical analysis of the data was performed using SPSS 20.0. Graphs were produced using Origin 2018 software. The Pearson correlation

method in SPSS 20.0 software was used to analyze the correlation between the number of single-flower visits and the number of stigma contacts for the honeybees and ground bumblebees on oil tree peony. Measurement data are presented as the mean $\pm$ standard error, and categorical data are expressed as percentages. Homogeneity of variances was tested using Levene's method. Independent t tests were used to compare the single-flower visit time, visit interval and number of visited flowers per minute between the honeybees and the ground bumblebees. The number of fruits per plant, number and weight of seeds per follicle, and number and weight of seeds per plant under different pollination treatments were compared using one-way analysis of variance (ANOVA) followed by a Bonferroni test. The kernel percentages, oil yield rates and compositions of seed oil for the different pollination treatments were compared using the nonparametric Kruskal-Wallis H method followed by a Dunn's multiple comparison test.

RESULTS

Foraging Behavior Parameters

Honeybees and ground bumblebees showed significant differences in the number of flowers visited per minute (independent-samples t test, $t=9.957$, $F=15.313$, $P<0.001$) (Fig. 2A), single-flower visit time ($t=-3.630$, $F=44.502$, $P<0.001$) (Fig. 2B), flower visit interval ($t=-9.072$, $F=104.792$, $P<0.001$) (Fig. 2C), and number of single-flower visits ($t=3.274$, $F=6.592$, $P=0.011$) (Fig. 2D).

The number of stigma contacts per flower by honeybees was 0-7, with an average of 0.92 ± 1.32 ; the stigma contact ratio of honeybees was 7.70% ($n=97$). Furthermore, honeybees exhibited a significant correlation between the number of single-flower visits and the number of stigma contacts per flower (Pearson $r=0.212$, $P=0.037$). The number of stigma contacts per flower by ground bumblebees was 0-5, with an average of 1.84 ± 1.06 . The stigma contact ratio of ground bumblebees was 24.11% ($n=63$) (Fig. 3), and there was a significant correlation

Fig. 2 The foraging behavior parameters of honeybees and ground bumblebees on oil tree peony flowers. A. number of flowers visited per minute. B. single-flower visit time. C. flower visit interval. D. number of single-flower visits.

Note: The data in the figure are the means $\pm$ standard errors. * $P<0.05$ and ** $P<0.001$ according to an independent-samples t test.

Fig. 3 The stigma contact ratios of honeybees and ground bumblebees. The upper limit of the rectangle is the 75th percentile of the data, the lower limit is the 25th percentile, and the middle line is the 50th percentile. The vertical length of the rectangle represents the quartile range, and the solid squares (points) are the observed values.

Fig. 4 The daily activity of honeybees (A) and ground bumblebees (B) on oil tree peony (the Y-axis on the left shows the number of flowers visited by honeybees, and the Y-axis on the right shows the air temperature in consecutive hours of observation)

between the number of single-flower visits and the number of stigma contacts per flower (Pearson $r=0.781$, $P<0.001$). There was a significant difference in the stigma contact ratio between honeybees and ground bumblebees (independent-samples t test, $t=-5.939$, $F=2.254$, $P<0.01$) (Fig. 3).

Daily Activity

The daily activities of honeybees and ground bumblebees are shown in Fig. 4. Honeybees left the nest later than ground bumblebees (after 8:00 vs. after 6:00), and their homing time was earlier than that of ground bumblebees (before 17:30 vs. before 19:00). The peak period of visiting flowers for honeybees was 9:30-11:45, during which the number of visited flowers was approximately 57.72% of the total number of flowers visited during the day. Between 9:30 and 11:45, the temperature was 27-31°C, and the relative humidity was 41%-60% (Fig. 4A). The peak period of visiting flowers for ground bumblebees was 6:00-10:00, during which the number of visited flowers was approximately 59.43% of the total number of flowers visited during the day. During this period, the temperature was 16-27°C, and the relative humidity was 48%-70% (Fig. 4B).

Pollination Efficiency Parameters

The four pollination treatments showed significant differences in the number of fruits per plant (one-way ANOVA, $df_{(3,789)}=2.931$, $P=0.033$), number of seeds per follicle ($df_{(3,3463)}=348.960$, $P<0.01$), seed weight per follicle ($df_{(3,3477)}=100.932$, $P<0.01$), number of seeds per plant ($df_{(3,379)}=55.974$, $P<0.01$), and seed weight per plant ($df_{(3,379)}=34.737$, $P<0.01$) (Tab. 1). Compared with the control, bee pollination significantly improved these indices (all $P<0.05$). Compared with honeybee

Table 1.
Effect of pollination by honeybees and ground bumblebees on the yield parameters and quality of oil tree peony (SE - standard error, n - number of samples)

Measurement index	<i>A. mellifera</i> (mean±SE (n))	<i>B. terrestris</i> (mean±SE (n))	Pollination without insects (mean±SE (n))	Field plot (mean±SE (n))
Number of fruits per plant	11.23±0.30 (311) ^a	10.51±0.27 (296) ^a	9.61±0.46 (90) ^b	10.95±0.50 (96) ^a
Number of seeds per follicle	36.44±0.55 (869) ^a	24.99±0.62 (866) ^b	15.92±0.36 (863) ^d	18.88±0.35 (866) ^c
Seed weight per follicle (g)	8.90±0.25 (872) ^a	7.45±0.24 (974) ^b	4.69±0.10 (865) ^d	5.25±0.14 (867) ^c
Number of seeds per plant	414.93±21.04 (98) ^a	281.46±15.93 (95) ^b	204.58±10.29 (90) ^c	152.34±10.48 (97) ^c
Seed weight per plant (g)	102.42±5.91 (98) ^a	75.57±4.13 (95) ^b	45.06±3.03 (90) ^d	57.30±2.96 (97) ^c
Kernel percentage (%)	66.92±0.002 (9) ^a	66.47±0.001 (9) ^a	66.13±0.002 (3) ^a	65.59±0.002 (3) ^a
Oil yield rate (%)	22.03±0.25 (9) ^a	21.72±0.33 (9) ^a	20.67±0.60 (3) ^a	21.10±0.31 (3) ^a

The data in the same row followed by different letters are significantly different at the 0.05 level (one-way ANOVA followed by a Bonferroni test or nonparametric Kruskal-Wallis H analysis).

Table 2.
Peony seed oil components (in %) obtained under different pollination treatments (mean±SE; SE - standard error)

Component	<i>A. mellifera</i>	<i>B. terrestris</i>	Pollination without insects	Field plot
Palmitic acid	5.98±0.07 ^a	5.93±0.02 ^a	6.00±0.04 ^a	6.00±0.04 ^a
Stearic acid	2.12±0.02 ^a	2.16±0.02 ^a	2.23±0.01 ^a	2.18±0.02 ^a
Oleic acid	22.9±0.15 ^a	23.4±0.02 ^a	23.4±0.00 ^a	23.9±0.10 ^a
Linoleic acid	24.37±0.23 ^a	23.5±0.38 ^a	22.7±0.10 ^a	23.2±0.00 ^a
α-Linolenic acid	43.97±0.39 ^a	44.37±0.09 ^a	44.3±0.10 ^a	44.2±0.00 ^a
Unsaturated fatty acids	91.34±0.06 ^a	91.53±0.58 ^a	91.66±0.00 ^a	91.56±0.11 ^a

The data in the same row followed by different letters are significantly different at the 0.05 level (Kruskal-Wallis H analysis).

pollination, ground bumblebee pollination caused a significantly larger number of seeds per follicle, seed weight per follicle, number of seeds per plant, and seed weight per plant (all $P < 0.05$). No significant differences in kernel percentage or the oil yield rate were observed between pollination treatments (Kruskal Wallis

H Test, $\chi^2=7.578$ $P=0.056$; $\chi^2=6.765$, $P=0.080$) (Tab. 1).

Palmitic acid, stearic acid, oleic acid, linoleic acid, α-linolenic acid, arachidic acid and arachidonic acid were detected as components of the peony seed oil. The unsaturated fatty acid content in peony seed oil was above 91%, and the relative

α -linolenic acid content was as high as 43%. The compositions of peony seed oil for the different pollination treatments are summarized in Tab. 2. There were no significant differences in palmitic acid ($\chi^2=3.167$, $P=0.367$), stearic acid ($\chi^2=6.514$, $P=0.089$), oleic acid ($\chi^2=5.227$, $P=0.156$), linoleic acid ($\chi^2=5.227$, $P=0.140$), α -linolenic acid ($\chi^2=6.649$, $P=0.084$), or unsaturated fatty acid ($\chi^2=4.006$, $P=0.261$) content between the different pollination treatments.

DISCUSSION

The activity of pollinators is affected by meteorological factors as well as physiological factors of the insects themselves. Temperature, humidity, and wind are key factors limiting bee feeding, and the effects of temperature on honeybee and ground bumblebee activity are greater than those of light, wind speed and other factors (Lee et al., 2016). Different bees display different pollination and pollen collection activities under different climatic conditions. Due to their weak phototaxis and low-temperature tolerance, ground bumblebees exhibit greater pollination activity than honeybees during periods of low temperature, rainfall and low light availability (An et al., 2007; Zhao et al., 2011; Lee et al., 2016). According to this study, ground bumblebees left the nest earlier than honeybees, and the peak activity of the former occurred between 6:00 and 10:00. Ground bumblebees are more tolerant than honeybees to low temperatures. When the temperature reached 29 °C in the morning, the number of ground bumblebees that left the nest for pollen collection greatly decreased. In contrast, honeybees left the nest after 8:00, with a peak activity period of 9:30-11:45. The results of this study suggested rather satisfactory complementary foraging behaviors. Oil tree peony has a short flowering period in early spring, when the temperature is low and the temperature difference between day and night is large. However, the effect of coapplying the two bee species for oil tree peony pollination remains to be explored.

The role of pollinators in the success of plant reproduction depends on their contribution to

the number of pollen grains deposited on the stigmatic surface and subsequent increases in fruit or seed yield and quality. In general, pollinator efficiency consists of visit density and such visit effects as the pollen-carrying capacity and the number of pollen deposited on the stigma per contact (Xie & An, 2014). On apple (*Malus domestica* Borkh.) blossoms, the numbers of pollen grains removed by honeybees and bumblebees were similar, but the amount of pollen transferred by *Bombus* spp. that settled onto the stigma was significantly higher than that transferred by honeybees. For almonds (*Prunus dulcis* L.), there was no difference in the amount of pollen transferred and settled onto the stigma between bumblebees and honeybees (Thomson & Goodell, 2001). Bumblebees interacted with more blueberry (*Vaccinium angustifolium* Ait.) flowers than did honeybees (Javorek et al., 2002). In the pollination of greenhouse peach (*Prunus persica* (L.) Batsch), bumblebee-transferred pollen settled more than did honeybee-transferred pollen, and the timing of fertilization after bumblebee pollination was earlier than that after honeybee pollination (Zhang et al., 2015). In this study, the stigma contact rates of both honeybees and ground bumblebees during pollen collection were low. Further studies on the amount of pollen transferred by bees onto stigmas as well as the mechanism underlying the fertilization of oil tree peony under such conditions need to be carried out.

The diversity and density of pollinators are factors that affect pollination efficiency (Sabbahi, DeOliveira, & Marceau, 2005; Atmowidi et al., 2007; Peña & Carabalí, 2018). At the time of alfalfa (*Medicago sativa* L.) pollination, the densities of honeybees and ground bumblebees were ten and five worker bees/m², respectively, and the pollination efficiency of ground bumblebees was higher than that of honeybees (Cecen, Gurel, & Karaca, 2008). In the pollination of greenhouse peach, the colony of ground bumblebees that contained 60-70 worker bees and the honeybee colony that contained 6,000 worker bees were compared. The pollination efficiency of the honeybees was greater than

that of the bumblebees (Zhang et al., 2015). The flowers of the oil tree peony are large, and the flowering period is short. In early spring, the number of pollinating insects is relatively small in the wild. Artificially increasing the number of insects may be an effective way of increasing the seed yield of oil tree peony.

Pollination is essential for spermatophytes and is the process by which pollen is transferred from the anther of the stamen to the stigma of the pistil. The seed-setting rate or seeding rate is usually used as a proxy for pollination success (Delaplane et al., 2013). Bee pollination not only increases crop yield but also improves quality and increases market value (Bommarco, Marini, & Vaissière, 2012; Said, Inayatullah, & Ali, 2017; Stein et al., 2017). For crops that rely on pollinators, pollination is directly affected by pollinator abundance (Sabbahi, DeOliveira, & Marceau, 2005; Peña & Carabalí, 2018). 'Fengdan' is a cross-pollinated plant, and its self-pollination rate is low (Han et al., 2014; Si, 2016; He et al., 2019). In this study, honeybee pollination greatly increased the yield of oil tree peony. Specifically, honeybee pollination increased the seed yield of oil tree peony by 78.74%, and ground bumblebee pollination by 31.88%. However, the oil yield and fatty acid content of oil tree peony seeds were not significantly improved. In this study, honeybees and ground bumblebees were encouraged to pollinate oil tree peony by setting up a pollination net room. The results showed that the seed-setting rate of plants pollinated by honeybees and ground bumblebees was higher than that of plants in the control and under natural field conditions, indicating that the technique was effective for pollinating oil tree peony. However, how to apply honeybees and ground bumblebees to oil tree peony in the field requires further study.

In conclusion, both honeybees and ground bumblebees can effectively improve the seed and oil yields of oil tree peony. Honeybees and ground bumblebees generally show complementary foraging behaviors in terms of time. The results of this study may provide useful insight for improving the seed and oil yields of large-scale-planted oil tree peony in the field.

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