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Research Article

Flower Constancy in the Generalist Pollinator *Ceratina flavipes* (Hymenoptera: Apidae): An Evaluation by Pollen Analysis

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The food habits of the solitary bee *Ceratina flavipes* were studied by observation on foraging behavior and identifying the pollen grains that they collected. It appeared that *C. flavipes* tend to collect pollen from particular species; however, they visit multiple flowering species. We analyzed pollen sources from pollen loads of dried specimens from single foraging trips (SFT) and in pollen balls created from a single foraging day (SD). The pollen from all pollen balls in a nest represented the harvest from an entire breeding season (BP). This analysis showed that each bee on average collected pollen from 3.24 (SFTs), 2.02 (SD), and 3.12 (BP) flowering species. Bees collected pollen from a total of 14 flowering plant species. Furthermore, we calculated when pollen balls were created and found no significant interaction between seasonal pollen availability and bee preferences. Moreover, bees had consistent flower preferences, even if the preferred flower was not dominant at all times. These results indicate that *C. flavipes* exhibits flower constancy, and therefore, the generalist pollinator *C. flavipes* could function like a specialist pollinator.

1. Introduction

Flower constancy means that a bee restricts its foraging activity to one or a few flowering species, even when many other flowers are available. Since the last century, flower constancy has been studied in honey bees [1–6], bumble bees [7–10], and a few other bee species [11–13]. Flower constancy is an important behavior because it can enhance pollination efficiency for the plant and foraging efficiency for the pollinator. In eusocial bees, enhanced foraging efficiency by individual workers improves the colony survival rate. Thus, flower constancy has been studied extensively in eusocial bees [2, 10, 11].

The mechanisms of flower constancy in bees have been studied empirically [14, 15] and theoretically [16, 17], but are still unknown. Cognitive ability, vision [10], olfaction [6, 8], and memory [3, 5, 18] are thought to influence flower constancy. In solitary bees, foraging efficiency is also likely important; their olfactory sense is highly developed. For example, the solitary bee *Lasioglossum figueresi* uses odor to recognize the nest [19]. Thus, solitary bees may also have flower constancy. Pollen balls provided for offspring by solitary bees have been examined in *Lasioglossum* [19], *Megachile* [12], *Heriades* [12], and *Osmia* [13]; most pollen balls of these species contain pollen from only two to three plant species, suggesting flower constancy in the preparation of the pollen ball. In these solitary bee species only the plant species used for pollen balls can be noted because no data on the available flowers were provided.

Previous studies of flower constancy in eusocial bee species did not examine temporal variation in flower constancy throughout the breeding period because many were laboratory-based studies. It is difficult to follow bees individually or to identify offspring age in the field, making laboratory studies advantageous. However, flower resources in the field might influence foraging behavior.

Therefore, we explored the relationship between the availability of flower resources and flower constancy in the solitary, generalist pollinator bee *Ceratina flavipes*. The life history of *C. flavipes* has been well studied in Japan [20–22].

We analyzed flower constancy based on pollen samples at three levels: a single foraging trip, a single day of foraging, and the entire breeding period. We defined flower constancy as when individual *C. flavipes* forages on fewer flowering species than the total number of plants used by all examined individuals of *C. flavipes* during the study.

2. Methods

2.1. Species and Study Site. *Ceratina flavipes* is the dominant species at the study site on the Ishikari Coast, Japan [23]. On the Ishikari Coast, a windbreak chaparral runs parallel to the shoreline, which is covered by a 200–300 m wide grassland vegetated by various wild flowering plants. Each female of *C. flavipes* digs a nest burrow in the stem of a dead grass shoot and oviposits several eggs during the breeding season. During the breeding season, females forage for pollen and nectar several times each day when weather conditions are suitable. Females make a pollen ball and lay an egg on it; the larva eats the pollen ball and grows within the cell. Generally, the female stores a pollen ball and an egg at each cell. The pollen balls and eggs are placed individually and in temporal order along the nest burrow. This behavior is advantageous because we can determine the order in which the eggs were laid. The breeding season of *C. flavipes* is from early June to late July in this study site.

The study site had about 22 flowering species, eight of which were observed in this study: *Calystegia soldanella* (Convolvulaceae), *Lathyrus japonicus* (Leguminosae), *Melilotus suaveolens* (Leguminosae), *Oenothera biennis* (Onagraceae), *Picris hieracioides v. glabrescens* (Compositae), *Rosa parvifolius* (Rosaceae), *Rosa rugosa* (Rosaceae), and *Vicia cracca* (Leguminosae). To study pollen resources used by *C. flavipes*, we placed 69 bee nests in the middle of a quadrate in the end of May 2000, before the bees started to oviposit. Set nests were collected from an area surrounding the study site.

2.2. Observation of Flower Visitation. A total of 13 nest-building female *C. flavipes* were followed and their foraging behavior observed from 8:00 to 14:00 on 18 and 20 June and 6, 7, and 11 July 2000. We observed marked bees as long as we could track them by eyes during observation periods (8:00–14:00). We then recorded (1) the flower species visited, (2) whether the individual moved between flowers within a plant, and (3) the behavior on the flower, which was classified into landing on the flower petals, staying on the central of flower without foraging pollen, and pollen foraging. For tracking observation, bees were caught and marked with paint marker at their abdomen. Each bee was marked with small dots of two colors and was identified by color combinations.

2.3. Pollen Analysis. We regarded the pollen load at the scopae of hind legs as the mean amount of pollen collected in a single trip. We regarded one pollen ball and all pollen balls in a nest as the mean amount of pollen collected in a single day and throughout a breeding season, respectively.

For the analysis of pollen collected in a single foraging trip, we used pollen attached to the scopae of 84 mounted specimens of bees sampled from several sites near the Ishikari Coast site in the past 10 years. These mounted specimens were caught at sites with more than two flowering plant species. Thus, we assumed that they had the opportunity to visit multiple plant species. To determine flower constancy within a single foraging trip, we used pollen loads from the pollen baskets of bee specimens that had been sampled at and near the study site within the last 10 years. We used dead specimens because collecting pollen loads from bees on each foraging trip would cause too much disturbance of the bee behavior.

For pollen collected in a single day or throughout the breeding period, we sampled 69 nests at the study site on 1 July 2000. We analyzed 253 pollen balls from these nests. When a pollen ball was already consumed by a larva, we collected the pollen ball particles and larval or pupal waste remaining in the cell.

We processed the pollen using the standard acetolysis method [24]. Pollen grains ($n = 200$) were randomly chosen from each sample and identified to species under a microscope, referring to technical pollen books [25, 26] and pollinic preparations. The pollinic preparations were samples of untreated pollen collected from flowers at the study site.

2.4. Estimation of Oviposition Date. *Ceratina flavipes* sequentially oviposits from the bottom upward in the nest. This behavior was used to estimate oviposition dates and the dates on which pollen balls were made. We divided the immature individuals into stages, and the developmental periods were allocated among the stages. Three larval stages were defined: "small larvae" whose legs were hard to identify (4 or 5 days after oviposition), "medium larvae" whose legs were easy to identify (11 to 13 days), and "large larvae" without a pollen ball (18 or 19 days). Eggs hatched within 1 or 2 days. Small larvae became medium larvae after 2 or 3 days. We used these developmental stages to back-calculate the oviposition dates of immature bees sampled from the set nests. We confirmed that the order of immatures in the nest and the pollen with each immature did not conflict with the phenological calendar. We recorded offspring stage (e.g., adult, pupa, larva, or egg) in order from the bottom of each nest. To determine the developmental period of each stage, we sampled 10 wild nests with immatures at the study site. After dissecting the 10 nests, each individual was placed in a vial with a pollen ball, kept at room temperature without air conditioning, and reared in the laboratory. For the hatching period, we selected the oldest and youngest eggs in the nest because we did not know when the eggs had been oviposited.

2.5. Available Pollen Resources and Flower Constancy. The availability of pollen resources in the field was compared with the pollen in the nests of individual bees from the pollen analysis. The availability was estimated by regularly counting the number of flowers and determining the average dry weight of pollen per flower in each focal species. We counted

Individual code	
1	-B-B-B-**B**-B-**B**-**B**-A=A-
2	-**A**=**A**-**A**=**A**=**A**-A-
3	-B-B=**B**=**B**=**B**=B-
4	-**B**-B-A-B=B-**B**-
5	-**B**-**A**-**B**-A-**B**-
6	-A-**D**=**D**-A-
7	-A-**D**=**D**-A-
8	-**A**-**A**-A-A-
9	-**C**-**C**=**C**-
10	-C-**E**-C-
11	-B-B-**B**-
12	-**A**-**A**-A-
13	-**A**-**A**-A-

Figure 1: Consecutive visits to flowers by marked *Ceratina flavipes* in late June 2000 at the study quadrat. Ishikari study site. Each alphabet indicate flowering species, A: *Rosa rugosa*; B: *Rosa parvifolius*; C: *Picris hieracioides v. glabrescens*; D: *Lathyrus japonicus*; E: *Calystegia soldanella*. And each marks indicated the behaviors, =: Moving within same stem; -: Moving to another stem. Bord face letter indicates collection of pollen, underline indicates staying at central of flower witout collecting pollen, and standard face letter indicates landing on the flower petals.

the number of open flowers of the eight focal species, treating the spicate of *C. soldanella* as one flower, within a 50 × 100 m quadrate once per week during the observation period (12 June to 1 July 2000). We also recorded the date of first flowering in each species. To calculate the average amount of pollen provided by a single flower per day, we selected several intact flower buds from each focal species at the edge of the study site (10 to 35 buds per species) and covered each bud with a small bag (3 × 4 cm) of fine mesh cloth. We collected five covered flowers every day from the start of flowering until petals dropped. Sampled flower heads were dried at room temperature, and the pollen was separated from other parts (i.e., anthers and petals) using a 1 mm wire mesh filter. The pollen was then completely dried in an incubator at 40°C for more than 1 week and weighed on an electronic balance.

3. Results

3.1. Flower Visitation. We successfully followed 13 marked bees and observed their flower visits (Figure 1). Although six bees visited two species, all *C. flavipes* individuals foraged exclusively for pollen on a particular species, except bee number 5 that collected pollen from two plant species.

3.2. Pollen Analysis. The 14 plant species found in the pollen analysis included the eight focal species. The mean (maximum in parenthesis) number of plant species was 3.24 (7), 2.02 (5), and 3.12 (6) for pollen collected in a single foraging trip (SFT), a single day (SD), and the breeding period (BP), respectively (Table 1). We found that the mean number of plant species visited was relatively low, with 55 (SFT), 227 (SD), and 50 (BP) of pollen load composed by more than 80% of same species, furthermore, some of them, 6 (SFT), 94 (SD), and 9 (BP), composed by 100% of same species within analyzed 200 pollen grants (Table 1). These results indicate that *C. flavipes* shows flower constancy, although it is a generalist pollinator. Flower constancy means that an individual visits some flowering species regularly, although, overall, different individuals of *C. flavipes* visit various flowering species to obtain resources.

3.3. Oviposition Date. Of the immature bees that we reared from 10 nests sampled in the field, 39 were female and 31 were male. Eggs and small, medium, and large larvae were oviposited on 30 June or 1 July; 26 or 27 June; 18, 19, or 20 June; and 12 or 13 June, respectively (Figure 2(b)). These results coincide with the pollen analysis and the phenology of the eightfocal plant species at the study site (Table 2, Figure 2(a)).

3.4. Available Pollen Resources and Flower Constancy. The pollen availability of each species was estimated as the product of the dry weight of pollen per flower head and the number of flowers (Table 3). The mean dry weight of pollen per flower decreased in the following order: *V. cracca*, *R. rugosa*, *R. parvifolius*, *M. suaveolens*, *P. hieracioides v. glabrescens*, *L. japonicus*, *O. biennis*, and *C. soldanella*. There was interspecific variation in the flowering period; the longest was that of *M. suaveolens* and the shortest was that of *C. soldanella* (Table 3). Pollen availability was not significantly related to bee flower preference at any developmental stage (Table 4; *G*-tests, egg: $X^2 = 9979.381$, $P < .01$; small larvae: $X^2 = 11782.85$, $P < .01$; medium larvae: $X^2 = 22632.59$, $P < .01$; large larvae: $X^2 = 24017.79$, $P < .01$).

In nine nests, all pollen balls in the nest were composed of a single plant species, that is, *R. rugosa* or *R. parvifolius*. Although *R. parvifolius* was not a dominant species at the beginning of the breeding season, three female bees constantly foraged on *R. parvifolius*.

4. Discussion

Flower gardens in temperate areas can be beautiful, because various species flower in a short period of time. In this study site, which was located in a cool-temperate area, 22 plant species flowered concurrently. There was interspecific variation in flower density with *R. parvifolius* being one of the rarest. Although a rare species might require a specialized pollinator, we did not observe specialist pollinators on 1 July. However, generalist pollinators can also function as specialized pollinators if they exhibit flower constancy. *C. flavipes* showed flower constancy in its pollen foraging (Table 1), and the intensity of its flower constancy seemed to vary intraspecifically.

We studied flower constancy of polylectic solitary bee, *C. flavipes* with observation of foraging behavior for SFT, pollen analysis from pollen attached specimens for SD, and that from pollen ball in the nest for BP. It is difficult to conclude with each result from SFT, SD, and BP, because there are some limitations due to the small number of foraging observations (SFT), uncertainty of foraging information of

Table 1: Composition of pollen grains ($n = 200$) randomly chosen from each of 84 pollen loads and 253 pollen balls.

Level of pollen load		The number of flowering species/pollen load		Percentage of pollen grains of the most dominated plant species within random 200 pollen grains			
	N	Range	Mean ± S.D.	100%	100 >∼≥ 80%	80 >∼≥ 50%	50 >∼> 0%
Pollen loaf	84	1–7	3.24 ± 1.27	6	49	26	3
Pollen ball	253	1–5	2.02 ± 0.91	94	133	25	1
Nest	69	1–6	3.12 ± 1.47	9	50	9	1

Table 2: Species of pollen grains contained in cells for each developmental stage collected on 1 July. +: present; −: absent; LL: large larva; ML: medium larva; SL: small larva; E: egg. Sum of set 69 nests and sampled 10 nests for determination of developmental period, was shown in this table.

Stage (no. of pollen ball)	Total no. of flowering sp.	Flowering sp.													
		Rr	Lj	Hr	Lm	Rp	Vc	Ob	Ph	Tp	Tr	Cs	Ms	Ea	Sa
E (17)	10	+	+	+	+	+	+	+	+	−	−	−	−	+	+
SL (12)	8	+	+	+	+	+	−	−	−	−	+	+	+	−	−
ML (52)	8	+	+	+	+	+	+	−	+	+	−	−	−	−	−
LL (93)	6	+	+	+	+	+	+	−	−	−	−	−	−	−	−

Rr: *Rosa rugosa*; Lj: *Lathyrus japonicas*; Hr: *Hypochoeris radicata*; Lm: *Lonicera morrowii*; Rp: *Rosa parvifolius*; Vc: *Vicia cracca*; Ob: *Oenothera biennis*; Ph: *Picris hieracioides*; Tp: *Trifolimu pretense*; Tr: *Trifolium repens*; Cs: *Calystegia soldanella*; Ms: *Melilotus suaveolens*; Sa: *Silene armeria*; Ea: *Erigeron annuus*.

specimens (SD), and lack of uniformity in estimation of flower availability (BP). However, these limitation needs to be dealt with in a separate studies, considering all the results together in this study, it is possible to regard *C. flavipes* to have flower constancy.

Ceratina flavipes tended to prefer certain plant species (Figure 1), these data are insufficient because observations were made were not tested experimentally. Our results, however, indicate a preference of *C. flavipes* for *R. rugosa* and *R. parvifolius* pollen at this study site (Table 4). Other flowering species were uncommon in pollen balls, although the availability of some species was high (Table 4). The uncommon species in pollen balls may result from bee behavior, such as casual landing or nectar feeding. Although the individual bees exhibited flower constancy, many flowering species were used (Figure 1). Thus, the percentage of pollen grains represented by the most dominant plant species was low (Table 1), indicating that bees may choose to collect pollen from a particular flowering species.

The mechanisms and causes of flower constancy in pollinators still remain elusive. Many conceptual and empirical studies suggest that the cognitive and memorization abilities of pollinators are important determinants of flower constancy. In theoretical studies, based on a classical patch model [27], optimal strategies with an important parameter, that is, individual memory, have been constructed [16, 17]. Bees have the cognitive ability to recognize floral colors [10, 28]; furthermore, the cognitive ability to recognize odors has been explored, especially in bumble bees [7, 8] and honeybees [3–6]. The memory of an individual forager is the primary contributor to flower constancy [18]. Previous studies have suggested that generalist pollinators are effective pollinators for angiosperms [29–31]. Flower constancy increases the effectiveness of pollination by generalist pollinators [32]. The various determinants of flower constancy are connected via neural substrates [33]. These factors are regulated by the highly developed sensory systems in the bees [4, 34, 35].

Flower traits (i.e., odor, color, and shape) might motivate bees to select certain flowers when foraging. In particular, olfactory sensations might be important, particularly for bees, because olfaction is used to find particular plant species [5, 6, 8] and to recognize the nest [19]. However, bees' ability to remember flower traits is limited; it is unclear how many flower traits bees can memorize and/or discriminate among when foraging. To determine the mechanisms of flower constancy in bees, the relationship between memorization and learning of particular plant species and the foraging behavior of the bees must be determined.

Although the lifecycles of some bee species are known, the timing of memorization and learning remain unclear. In *C. flavipes*, prior studies describing the life cycle indicate that individuals have opportunities to memorize pollen species at different developmental stages: when growing on a pollen ball provided by the mother, when they eclose with frass in the cell, when they are provided with nectar and pollen by their mother or elder sisters after the breeding season, when they first forage by themselves during dispersal in the prehibernation season, or when they start foraging by themselves at the beginning of the nesting and/or breeding season after hibernation [23, 36–39]. Holometabolous insects have different nervous systems as adults than they do as juveniles [40]; thus, memories acquired as a juvenile may be lost during metamorphosis. Combined with the results of prior studies, our results suggest that the memorization required for flower constancy is more likely to occur in the prehibernation season, that is, the period from emergence to hibernation, than in other stages.

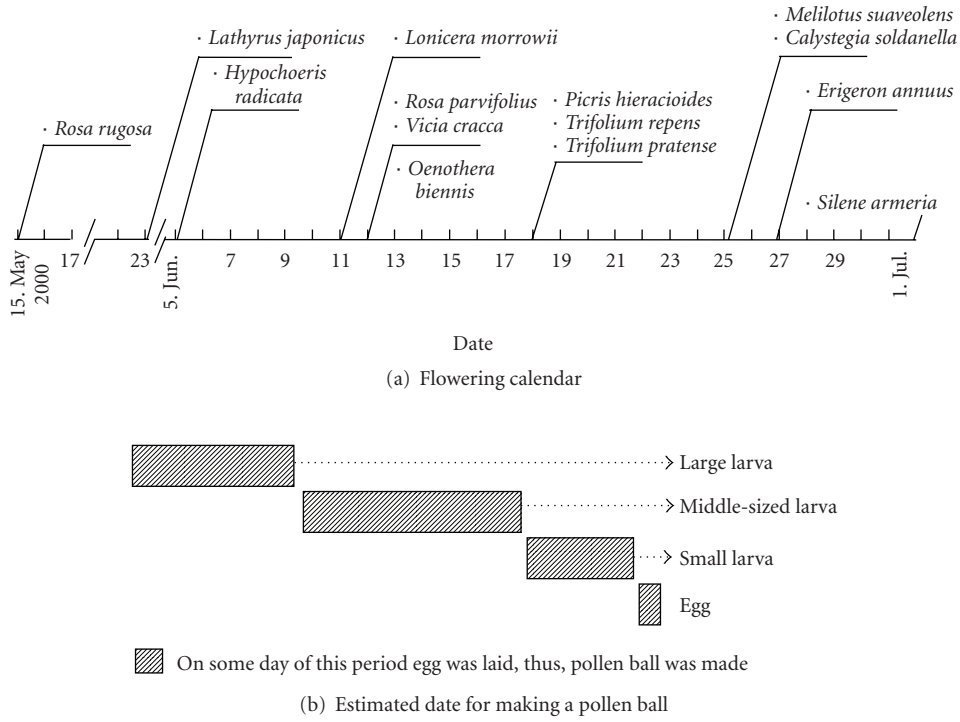

Figure 2: (a) Flowering phenology on the Isikakri Coast and (b) oviposition dates (i.e., dates when pollen balls were made) inferred from the rearing of immature individuals in the laboratory. Nests with pollen balls, eggs, larvae, pupae, and adults were sampled on 1 July. The thick line in (a) represents the starting dates of the flowering period of each flowering species at the field. The date axis in (a) is common with in (b).

Table 3: Weight (mg) of desiccated pollen per flower head on each day after the initiation of flowering (see Figure 2(a) for each species). Mean ± standard deviation of five flower heads. Average pollen production (P) was used to calculate pollen availability within a 50 × 100 m quadrat (cf. Table 4). Names of flowering species are arranged in descending order average pollen production.

Flowering sp.	Days from the initiation of flowering							Average pollen productin (P)
	1	2	3	4	5	6	7	
Vicia cracca	33.26 ± 41.9	34.30 ± 18.61	22.83 ± 9.11	33.50 ± 47.46	19.34 ± 30.77	13.55 ± 3.64	—	26.13 ± 8.80
Rosa rugosa	26.96 ± 22.14	13.48 ± 14.98	9.38 ± 4.03	4.22 ± 3.54	2.53 ± 0.92	—	—	11.31 ± 9.76
Rosa parvifolius	12.60 ± 8.59	15.48 ± 13.56	9.25 ± 32.51	7.72 ± 3.29	—	—		11.26 ± 3.47
Melilotus suaveolens	1.99 ± 1.42	3.05 ± 1.24	10.00 ± 1.65	13.04 ± 4.13	18.22 ± 8.33	9.05 ± 1.92	3.42 ± 16.58	6.76 ± 4.54
Picris hieracioides	8.15 ± 1.87	4.58 ± 2.13	2.95 ± 1.49	2.64 ± 1.81	—	—	—	4.44 ± 2.20
Lathyrus japonicus	0	11.84 ± 30.67	0	0				2.96 ± 0.00
Oenothera biennis	0.58 ± 0.24	1.97 ± 1.68	0.93 ± 0.54	—	—	—	—	1.15 ± 1.16
Calystegia soldanella	4.41 ± 0.95	0.45 ± 0.30	—	—	—	—	—	0.93 ± 0.84

Our quadrate was near the maximum size in this study area, but there are some small vegetation patches around the study area, such as parking areas. The *V. cracca*, *R. parvifolius,* and *P. hieracioides* pollen were found from pollen balls; however, we did not observe these plant species at the study area during the putative period (6/12-13) (Table 4). The results suggested that the bee might forage beyond our study quadrate to seek for the particular flowering species. Furthermore, a species might be memorized before hibernation, the first foraging period of *C. flavipes*, as the olfactory information acquired in the early days after emergence modifies bees' later behavior in honeybee [18].

Table 4: Comparison of pollen availability and pollen usage by *Ceratina flavipes* and Phenology of the total dry weight of pollen for each flowering species during the breeding season of *C. flavipes*. The number of flowers is shown in parentheses. Total pollen mass was calculated as $m \times n$, where m is the average dry pollen weight per flower (from Table 3) and n is the number of flowers. Availability and usage differed significantly among species.

	Number of pollen grants (Number of flower head)							
Flowering sp.	Availability	Using [83 balls]	Availability	Using [47 balls]	Availability	Using [8 balls]	Availability	Using [10 balls]
	6/12-13	LL	6/18–20	ML	6/26-27	SL	6/30–7/1	E
Vicia cracca	0.00	106	2351.70 (90)	5	9145.50 (350)	0	12542.40 (480)	1
Rosa rugosa	7227.09 (639)	9372	51256.92 (4532)	5602	44991.18 (3978)	981	6853.86 (606)	979
Rosa parvifolius	0.00	4666	371.58 (33)	2546	675.60 (60)	518	35941.92 (3192)	794
Melilotus suaveolens	0.00	0	0.00	0	1453.40 (215)	0	17778.80 (2630)	0
Picris hieracioides	0.00	73	972.36 (219)	55	1602.84 (361)	0	5772.00 (1300)	6
Lathyrus japonicus	4091.49 (1521)	90	13619.47 (5063)	41	4040.40 (1365)	0	515.04 (60)	0
Oenothera biennis	0.00	0	0.00	0	1.15 (1)	0	623.3 (542)	0
Calystegia soldanella	0.00	0	16.86 (2)	0	0.00	0	1.41 (8)	0
others	0.00	2293	2205.64 (759)	1151	0.00	101	111.18 (631)	220
G-test	$X^2 = 24017.79$		$X^2 = 22632.59$		$X^2 = 11782.58$		$X^2 = 9979.381$	
	$P < .01$		$P < .01$		$P < .01$		$P < .01$	

These facts together suggest that the foraging behavior of adults is determined by adult experiences in the pre-hibernation season. However, this may not always be the case. *C. flavipes* is also found in temperate areas, where it is unlikely that bees use information memorized before hibernation because the flowering species are completely different at the beginning and ending of the breeding period. In addition, many solitary generalist bees eclose only after hibernation [12, 19, 41–43]. To determine the mechanisms of flower constancy in solitary, social, and generalist bees, the relationships between learning, memorization, and forging behavior should be examined using behavioral observations and neurobiological methods.

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