Foraging Characteristics of a Solitary Bee, Andrena taraxaci orienticola

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Abstract

Here, I aimed to reveal the foraging habits of *Andrena taraxaci orienticola* females. I found the following results: 1) This bee is oligolectic and use four Asteraceae as food plants, primarily relying on *Taraxacum platycarpum*; 2) Bees begin visiting *T. platycarpum* at the flower opening, abandoning them a few hours later, although the flowers are still open; 3) Bees shift visitation to *T. platycarpum* from sunny to shaded sites as time passes; 4) Most flights were made between 08:00 and 11:00 h; 5) They collect pollen in most flights, except for the first flight of the day; 6) Generally, bees make 4.7 flights of 18.4 min at intervals of 6.0 min; 7) Bees do not add nectar to pollen loads in the field.

Keywords : food plant, foraging pattern, insect-plant interaction, pollen, Taraxacum

Introduction

Approximately 18,000 described bee species compose the seven families of Apoidae in Hymenoptera (Michener, 2000). They have various social levels, from solitary to eusocial, but most are solitary (Danforth et al., 2019). Solitary bees are distributed over multiple environments, from the tropics to the northern polar region. Except for parasitic species, female bees build nests into which they bring nectar and pollen from flower patches. These food materials are mixed together to form ball- or loaf-like masses as food for larvae in the nest. Before being stored, some of them may also be consumed by females as a source of energy and proteins for further foraging and egg production. Different food source plants are used depending on the species. Generalist bees use various flowering plants as pollen sources (polylecty). Other species are specialists with narrower food source ranges. They either use a few related plant spices

(oligolecty) or only one species (monolecty).

Solitary bees have diverse foraging characteristics and are adapted to environments with unique biotic and abiotic factors (e.g., climates, vegetation, competitors, and natural enemies). They are suitable subjects for studying the diversity of animal behavior and behavioral adaptation to environments. Still, their foraging habits are yet to be documented in most bee species.

Here, I investigated *Andrena taraxaci orienticola*, an abundant solitary bee on the campus of Tamagawa University, to obtain basic information on its foraging habits. I studied individuals regarding their 1) food plants, 2) temporal relationships with the blooming of food plants and the visiting bees, 3) temporal pattern of foraging, and 4) nectar addition to the pollen load for adhesion.

Materials and Methods

Bees and study sites

An aggregated nest site of *A. taraxaci orienticola* was found on the campus of Tamagawa University in 2015. All observations and experiments were performed in this nest site or its surroundings (Fig. 1).

Survey of food plants

I recorded the flowering plant species *A. taraxaci orienticola* visited during a route census. The census was conducted along a 250-m long route on the university farm adjacent to the aggregated nest every 30 min from

07:00 h to 12:00 h on April 19, 2015. Food plants were identified based on the description in references (Satake et al., 1981; Shimizu, 2003).

Relationships between the time of blooming and the visitation of bees

The Japanese dandelion *Taraxacum platycarpum* is a significant food plant for *A. taraxaci orienticola*. I recorded temporal changes in the flowering stage of *T. platycarpum* and the number of female bees visiting it to reveal the temporal relationships between the opening of flowers and the visitation of *A. taraxaci orienticola*. The survey was performed in an area where many *T. platycarpum* bloomed, \sim 5–20 m apart from the aggregated nest site (Figs. 1 and 2).



Figure 1 (A) An aerial photograph of the study site. Solid (blue) line, census route; Solid (red) area, observation site for visitation of Andrena taraxaci orienticola to Taraxacum platycarpum; N, nest site of A. taraxaci. Image source, Google Maps. (B) Nest site of A. taraxaci orienticola (indicated by a dashed circle).



Figure 2 Observation site for visitation of Andrena taraxaci orienticola to Taraxacum platycarpum.

During the survey, I chose 25 flower heads of *T. platycarpum* at the sunny and shaded sites. I recorded the flowering stage for each flower head every 30 min, from 06:30 h to 15:00 h on 12, 15, and 16 April 2015. There were four flowering stages: 1) closed flower head, 2) partially opened flower head with an opening angle of ligulate flowers of < 60 degrees, 3) partially opened flower head with an opening angle of 60-180 degrees, and 4) fully opened flower with an opening angle of > 180 degrees. The number of visiting *A. taraxaci orienticola* females found on *T. platycarpum* flowers was also recorded every 30 min at both sunny and shaded sites. The sunny and shaded sites contained 194 and 328 flower heads, respectively.

Video recordings at the nest site

I recorded the departure and return of the female bees to their nest with a video shoot to determine their temporal foraging pattern. I calculated the mean number of flights/ bee/day, flight duration, and the interval between flights. I made the video recordings on 3 and 6 April 2015 and 7, 11, and 15 April 2021. I recorded the activities for 11 and 15 nests in 2015 and 2021. I recorded some nests for two days. I made color markings on the bee thoraces for individual identification in 2021 to investigate whether females share their nests. I obtained air temperature at the Fuchu station of the Japan Meteorological Agency (\sim 12 km apart from the study site) during the observation period from https://www.data.jma.go.jp/obd/stats/etrn/index.php. I assumed the data were the air temperature at the study site.

Measurement of sugar contents of pollen loads

Some bees add nectar to foraged pollen grains to stick each other upon building pollen loads, but others do not. I investigated whether *A. taraxaci orienticola* does so or not. I obtained *A. taraxaci orienticola* pollen loads from captured females and compared sugar contents between pollen loads and pollen directly collected from *T. platycarpum*. This procedure was to investigate whether *A. taraxaci orienticola* added nectar to pollen loads. Pollen loads with nectar were expected to have higher sugar content than pollen alone. I measured the sugar content of pollen loads from the honeybee, which add nectar to their pollen loads (Parker, 1926). I captured females carrying pollen loads that returned to the nest with the insect net, placing them individually in plastic cylinders (diameter \times height, 4.5 \times 6.0 cm; Fig. 3) from 9 to 18 April 2015. I transferred the bees into the dark and collected pollen loads after they unloaded the pollen loads.

I also collected pollen directly from *T. platycarpum*. I gently rubbed their flower heads with a paintbrush in the laboratory to collect dropped pollen. I regarded pollen samples from different sites or on different days as different samples. One pollen sample was obtained from approximately 30–60 flower heads.

I collected honeybee pollen loads using a commercial pollen trap (Kumagaya Apiary, Saitama, Japan) from an *Apis mellifera* colony on the campus apiary in the summer of 2014. These pollen loads were stored at -20° C until the experiment. I examined the pollen grain morphology of all samples under a microscope, measured them, and identified them as the crape myrtle, *Lagerstroemia indica*.

I employed the following procedures to measure the pollen sugar content. After drying at 100° C for 4 h, I weighed the pollen load samples. I placed the samples



Figure 3 An Andrena taraxaci orienticola female was confined in a plastic cylinder to collect pollen loads.

individually in 1.5 μ l tubes and added 100 μ l water. After vortex for 5 sec, I centrifuged them at 10,000 rpm for 5 min. I collected the supernatant and measured the total sugar concentration (w/w) using a refractometer (1T, Atago Co. Ltd., Tokyo, Japan). Assuming that all sugars were dissolved in water, I calculated the sugar content of the pollen load samples from the sugar concentration and weight of the solvent (sugar concentration x 100 mg). I divided this value by the dry weight of the sample to calculate the sugar content per 1 mg of dry pollen.

Statistical analyses

In the survey for the relationship between the time of blooming of dandelion and visitation of bees. I compared the number of visits between the first and second halves of the flowering period by the binomial test, to determine whether the visitation of bees concentrated in a period soon after blooming started. The flowering period of dandelion was defined as a period with more than one flower head showing stage 2 or higher. The difference in the time of visitation between the sunny and shaded sites were tested by the Mann-Whitney's *U*-test.

In the survey of temporal pattern of foraging, I investigated the relationship between the time of day and flight duration with regression analyses. I applied the Davies test to examine whether the slope of the regression line was constant. When the constancy of slope was rejected by this test, I performed the 2-segmented regression analysis using the "segmented" package in R (R CoreTeam, 2015).

I used the Steel-Dwass test to determine differences in the sugar content for pollen loads and pollen directly collected from flowers.

Results

Route census for food plants

I recorded 364 visits of *A. taraxaci orienticola* on Asteraceae, *Ixeris japonica, Sonchus oleraceus, Taraxacum officinale*, and *T. platycarpum*. Nearly 84.5% were visitations to *T. platycarpum*, which peaked at 10:00 h and then declined (Fig. 4).

В

Relationships between the opening of the *T.* platycarpum flower and the visitation of *A. taraxaci* orienticola

The patterns in flower opening and visitation found on 12 April 2015 are shown in Figure 5. The flower heads started to open at 07:30 h and were completely opened at 09:30 h. The visitation by *A. taraxaci orienticola* synchronized with the flower opening, which peaked at 08:30 h and then declined. The visitations were concentrated just after the opening of the flowers. I found this trend in the other observation days (Table 1).

T. platycarpum delayed opening flower heads at the shaded site compared to the sunny site (Fig. 5). Visitation by *A. taraxaci orienticola* was also concentrated in the first half of the flowering period (Table 1). Only a few or no



Figure 4 (A) The number of Andrena taraxaci orienticola found in a route census and the plants they visited.
(B) A. taraxaci orienticola females visiting Taraxacum platycarpum.

female bees were observed on the flowers in the second half of the flowering period, although the flowers were still open. The visitation by *A. taraxaci orienticola* was earlier at the sunny site than at the shaded site, according to Mann–Whitney's *U*-tests (Table 1).



Figure 5 Temporal changes in the flowering stage of *Taraxacum platycarpum* and the number of *Andrena taraxaci orienticola* females found on *T. platycarpum* flowers at sunny or shaded sites. (E) Air temperature is shown in the lowest panel.

Days		No. A. taraxiaci found	No. A. taraxiaci found on T. platycalpum			
		1 st half of flowering period ^a	2 nd half of flowering period ^a	Significance ^b	(time of day)	
12 April 2015	(Sunny site)	30	0	<i>P</i> < 0.001	8:30	
	(Shaded site)	33	0	P < 0.001	9:30	
	Significance ^c				P < 0.001	
15 April 2015	(Sunny site)	22	0	<i>P</i> < 0.001	8:30	
	(Shaded site)	10	2	P < 0.05	10:00	
	Significance ^c				P < 0.001	
16 April 2015	(Sunny site)	14	0	<i>P</i> < 0.001	8:30	
	(Shaded site)	15	0	P < 0.001	9:00	
	Significance ^c				P < 0.001	

Table 1 Temporal changes in the foraging activity on Taraxacum platycalpum by Andrena taraxaci orienticola

a Flowering period was defined as a time period when more than one flower-head was scored as grade 2 or higher. If T. platycalpum was still blooming at the end of observation period (15:00h), the end of flowering period was defined as 15:00h.

b Binomial test

c Mann-Whitney's U-test

Temporal pattern of foraging flights

Most A. taraxaci orienticola females started to fly at 07:30 -08:30 h and ended at 10:00-11:00 h (Fig. 6). Except for a few trips, females brought pollen loads to nest on most trips. The females made several flights daily, although some flew only once and did not bring pollen loads (e.g., nests D2, G4, H2, J3, and Q on 3 April 2015 in Fig. 6). Even when females made several flights a day, sometimes they returned without pollen loads on their first flight. The flight duration of the first flight of the day was shorter for nonpollen trips than for pollen trips (Mann-Whitney's *U*-test : n = 9, 25, z = 2.71, P < 0.01). The interval after the first flight was significantly longer when females did not bring pollen loads than when they did (Mann-Whitney's *U*-test : n = 11, 19, z = 2.86, P < 0.01).

I investigated the relationship between the time of day and flight duration with regression analyses for daily

pollen trips recorded on 3 and 6 April 2015. The 2021 sample data was not used in the analysis as it was too small. The null hypothesis that the slope of the regression line was constant was rejected for each data set of the two days (3 and April 06, 2015) (Davies test, P < 0.001 each). Thus, I performed the 2-segment piecewise regression analysis. The flight duration decreased until 09:29 h (3

Table 2 Summary of 2-segmented regression analysis for flight duration associated with time of day in Andrena taraxaci orienticola females. Linier regression lines with different slopes (β 1 and β 2) meet at a breakpoint (BP).

Date	BP	Slope $\beta 1$	Slope $\beta 2$	Intercept
2 Apr. 2015	9.486	-40.035***	0.902###	394.017***
	(9:29)			
6 Apr. 2015	8.249	-47.07**	6.17###	399.02***
	(8:15)			

** P < 0.01; *** P < 0.001

*** Significant difference between slope β 1 and slope β 2 (Davies test, P < 0.001)

 Table 3
 Variables related to the temporal pattern of foraging in Andrena taraxaci orienticola.

	Pollen flights +	Ν	Pollen flights	Ν	Non-pollen	Ν
	non-pollen flights				flights	
No. of trips /bee /day (mean ± SD)	4.7 ± 2.19	29 ^a	4.1 ± 2.49	29 ^a	0.6 ± 0.62	29 ^a
Duration of foraging trip (mean ± SD) (min)	18.4 ± 12.67	209 ^b	18.0 ± 12.14	185 ^b	21.6 ± 16.13	24^{b}
Duration between foraging trips (mean ± SD) (min)	6.0 ± 8.79	162 ^b	4.2 ± 1.70	148 ^b	NA	
^a Number of bees						

b Number of trips or intervals

NA, not analyzed

April 2015) or 08:15 h (6 April 2015). Turns increased or became constant after that (Fig. 7, Table 2).

The means, duration, and interval of flights are shown in Table 3. In 2021, I color-marked all females I observed, except for a female from nest 13 (Fig. 6), to investigate whether females shared their nests. The bees did not share their nests. In addition to these nests shown in Fig. 6, I made preliminary observations for 10 nests with colormarked females. I did not observe several females using a single nest in those observations, although the data were not shown because of the incompleteness of the record (e.g., records for some flights were lacking).



Figure 6 Temporal pattern of foraging flights in *Andrena taraxaci orienticola* females. Filled rectangles indicate foraging (pollen or non-pollen) trips.



Figure 7 Temporal changes in the air temperature and flight duration of *Andrena taraxaci orienticola* females. Two-segmented regression analysis was performed based on the data of pollen flights for the time of day, flight duration, and regression lines were presented as solid lines.

Sugar content of pollen loads

The mean sugar content of *A. taraxaci orienticola* pollen load was 0.27 mg/mg, identical to that of *T. platycarpum* collected directly from flowers (0.27 mg/mg). There was no significant difference between the pollen from each group (Steel–Dwass test, P > 0.05; Fig. 8). Nonetheless, the sugar content of honeybee pollen loads was 0.49 mg/mg, significantly higher than that of *A. taraxaci orienticola* pollen loads (P < 0.05).

Discussion

Food source plants

A. taraxaci orienticola are oligolectic for Asteraceae species, and *T. platycarpum* is their primary food source plant, concentrating more than 80% of their flower visits. As I investigated food plants for only one day, I cannot exclude the possibility that the bees visit other plants in the additional period. However, the active period of this bee is approximately one month, overlapping the blooming period of *T. platycarpum* (personal observations). Further investigations on food source plants (e.g., analysis of pollen loads) are needed to clarify the feeding habits of this bee species.

Relationships between the opening of *T. platycarpum* flowers and the visitation of *A. taraxaci orienticola*

A. taraxaci orienticola limited visitations to T. platycarpum for a short time after flower opening. At least two



Figure 8 Sugar content in pollen loads and pollen directly collected from *Taraxacum pratycarpum*. Different letters on bars indicate significant differences in the Steel-Dwass test. n, Sample size.

explanations are possible for their reduced visitation to flowers that have opened for a long time. First, they might avoid depleted flowers. Nectar and pollen may be depleted shortly after flower openings due to frequent visits by bees. Second, bees might avoid high temperatures in flowers late in the day. Flower temperature could increase due to the sun's radiation (Corbet & Huang, 2016), and some bees may avoid heated flowers. Although the air temperature was not high during my observations, moderate heat could inhibit the activities of cool-adapted insects. *A. taraxaci orienticola* females are adapted to cool environments as they are active at low temperatures (e.g., Figs. 5 and 7).

Temporal pattern of foraging flights

I observed that bee foraging was concentrated from 08:00 h to 11:00 h in *A. taraxaci orienticola*, with substantial daily variations. This is consistent with the time the bees were found in *T. platycarpum*, not contradicting the hypothesis that the plant is their primary food source.

A. taraxaci orienticola females made 4.7 flights of 18.4 min at intervals of 6.0 min a day, returning to the nest with pollen loads in most flights. This short flight duration suggests the proximity of the foraging site to the nest. They probably only unloaded the forage and did not engage in nest activities [e.g., building larval provisions (pollen balls)].

Females often returned to the nest without pollen loads during the first flight of the day. In these cases, they might fail to forage. The relationship between the time of day and flight durations showed the need for long flights to forage pollen in the early morning. Females not carrying pollen loads might not have sufficient fuel to sustain foraging flights. It might be challenging to obtain nectar from *T. platycarpum* early in the morning. Nectar secretion of a closely related species, *T. officinale*, is scarce in the morning (Szabo, 1984). Solitary bees probably use nectar collected on the previous day as fuel with less nectar availability by keeping it in their crop. If insufficient fuel is carried, they may return to their nest before collecting pollen. Then, they might stay in the nest until the nectar is more abundant in the flowers. In line with this, the flight interval was relatively longer after a nonpollen trip than after a pollen trip. However, this study does not exclude the possibility that females always access nectar in flowers because the nectar availability remains unknown in *T. platycarpum*. Future study should examine whether females are indeed suffered from a shortage of fuel in the early morning.

Different hypotheses may explain nonpollen flights of females making a single flight in a day, as those females left for the flight later when nectar may be more available. These may be fueling flights. Even when they perform domestic work, such as constructing brood cells, they need fuel to continue working or for future flights. They may collect nectar in some nonpollen trips, as argued for other solitary bee species (Velthuis et al., 1984).

Although the pattern of pollen foraging is documented, that of nectar foraging remains unknown. It is possible that females always collect nectar whether they collect pollen or not in the foraging trip. However, their nectar collection should be associated with pollen collection because, unlike social bees, solitary bees have no means for storing nectar alone and must mix nectar with pollen in the nest for storage. In other words, they should collect enough amount of pollen before collecting nectar as larval food. They also need to collect some nectar after collecting pollen to build a pollen provision-mass. These constraints may be an important factor to determine the pattern of nectar and pollen foraging.

There was no evidence of sharing a nest with more than two females. Although I did not color-marked females individually, I did not observe any sign of nest sharing, such as two successive departures or returns in 2015. I confirmed this observation with individual color markings in 2021, which is consistent with the results of previous *Andrena* studies (Danforth et al., 2019).

Does A. taraxaci orienticola add nectar to the pollen load?

The sugar content of *A. taraxaci orienticola* pollen loads was similar to that of pollen directly collected from *T. platycarpum* flowers. Honeybee pollen loads formed by adding nectar (Parker, 1926) had significantly high sugar content, as reported in a previous study (Roulston et al., 2000). This indicates that *A. taraxaci orienticola* does not add nectar to collect pollen to build pollen loads. This species produces pollen loads in the scopa located on their tibia and other body parts, unlike honeybees, which use their corbiculae. The scopa of this species can probably hold pollen without added nectar, giving adherence to pollen grains.

Concluding remarks

Here, I provided information on the foraging of *A. taraxaci* orienticola females. Several questions may be asked from the results. Why do the bees not visit *T. platycarpum* flowers that have opened for a long time? Why do they make nonpollen trips? Why do they change flight duration according to the time of day? Consequently, the foraging behavior of this species would be understood more deeply by answering these questions.

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