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Bumblebee visits to *Impatiens* spp.: pattern and efficiency

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Summary. Three Japanese species of *Impatiens*, which secrete nectar continuously in long spurs, were visited by *Bombus diversus* workers consecutively throughout the day. *B. diversus* workers showed characteristic patterns of behavior in flower use, flower choice, and patch departure. (1) Bumblebees stayed longer on a flower which had been unvisited for a while than on a flower which had been visited recently. (2) Bumblebees preferred visiting flowers which had been unvisited for a while to visiting those which had been visited recently, and to visiting those which had been unvisited for a long period. (3) Bumblebees had a higher probability of leaving a patch after they had stayed on a flower for a short period than after they had stayed for a longer period. The bumblebees appeared to perceive both remotely and proximately chemical cues deposited by other foraging individuals, which indicated nectar rewards in a flower, and thus obtained a higher nectar intake than the mean amount of nectar left in a flower.

Key words: *Impatiens* – Bumblebee – Foraging – Flower choice – Nectar intake

Individual flowers that are visited by nectar-gathering bumblebees are highly heterogeneous in the amount of nectar they contain, due to intermittent depletion of nectar at every bumblebee visit (Heinrich 1975, 1979; Waddington 1981; Zimmerman 1982). Under such conditions, how do bumblebees visit flowers and how much nectar do they gather? Bumblebees foraging in single-species patches have been shown to choose among patches of plants (Hartling and Plowright 1979; Hodges 1981), and among individual flowers (Heinrich 1979; Cameron 1981; Waddington et al. 1981; Thomson et al. 1982; Zimmerman 1982; Marden 1984). Behaviors indicating optimial patch use and flower choice have been observed only under experimental conditions and not yet under field conditions where foraging bumblebees themselves govern the amount of nectar in each flower. To examine the relationship between the fluctuation in amount of nectar and bee foraging behavior, I conducted a field study on the *Impatiens* – bumblebee system.

Japan has three *Impatiens* species: *I. textori, I. hypophylla*, and *I. noli-tangere*. The flowers of the former two are purple; those of the last are yellow. Every species had pendent, chasmogamous, perfect, zygomorphic, protandrous flowers with long nectar-secreting spurs. They secrete nectar continuously and are commonly visited and pollinated by nectar-gathering workers of a long-tongued bumblebee species, *Bombus diversus*. The *Impatiens* – *B. diversus* relationship is a coevolutionary system. I observed the foraging behavior of *B. diversus* on *Impatiens* in the field, and examined the decision-making process and the rate of nectar intake that resulted from their foraging strategy.

Materials and methods

I investigated the flowering biology of *Impatiens textori* in the field at Kibune, Kyoto prefecture, Japan. The flowering patterns of 44 individual flowers of *I. textori*, (life span and sexual composition of individual flowers), were observed during 4–8 September 1982. Nectar secretion of *I. textori* was monitored at Kibune from 30 September to 1 October 1982. Ten flower buds that had been expected to open within a few hours were enveloped in niron bags at 0500 h on 30 September 1982. The volume of floral nectar secreted in a spur was measured with a microcapillary tube every few hours till 1700 h on 1 October, when most of the flowers fell off. The sugar concentration of the nectar samples was measured with a refractometer.

I observed the diurnal foraging behavior of *B. diversus* individuals visiting clumps of flowers of *Impatiens textori* (T1–T4), *I. hypophylla* (H1) and *I. noli-tangere* (N1); dates and sites of the observations are shown in Table 1. The site at Kibune is along a valley surrounded by *Juglans*-dominated temperate deciduous forest. During observations T1–T4, *I. textori, Leucosceptrum stellipilum, Cirsium microspicatum, Isodon longitubur, Polygonum thumbergii*, and *Liguraria fischeri* were in bloom. At observation N1, *I. noli-tangere, Hydrangea macrophylla*, and *Actinidia arguta* were in bloom. The Mt. Tsutsujo sites is along a valley in *Fagus*-dominated temperate deciduous forest. At observation H1, *I. hypophylla* and *L. stellipilum* were in bloom. Figure 1 shows the distribution of clumps of flowers at T1–T4, H1, and N1.

I observed the diurnal foraging behavior of *B. diversus* visiting these clumps of flowers, which I henceforth call a patch. The patches selected for observations were oblong so that all flowers in a patch could be seen from the observer's position in front of the patch. The size of each patch and the number of flowers in it are listed in Table 1. Before commencing observations, I drew a map of the flowers in the patch on white pastebroad. On sheets of tracing paper superimposed on the flower map, I recorded the time at

Table 1. The dates, study sites, and selected patches for six days of observation of bumblebee visits

Observation code	Date	Weather	Site	Location	Altitude (m)	Patch size (m)	Number of flowers
T1	5 Sep 82	Fine	Kibune	Kyoto, Kyoto Pref.	470	1.5 × 1.0	18
T2	8 Sep 82	Fine	Kibune	Kyoto, Kyoto Pref.	470	1.5 × 1.0	29
T3	13 Sep 82	Cloudy/Fine	Kibune	Kyoto, Kyoto Pref.	470	1.5 × 1.0	23
T4	22 Sep 82	Fine	Kibune	Kyoto, Kyoto Pref.	470	1.5 × 1.0	23
H1	17 Sep 82	Cloudy	Mt. Tsutsujo	Tosa-gun, Kôchi Pref.	1570	2.0 × 1.2	27
N1	9 Jul 83	Cloudy	Kibune	Kyoto, Kyoto Pref.	460	2.2 × 1.0	11

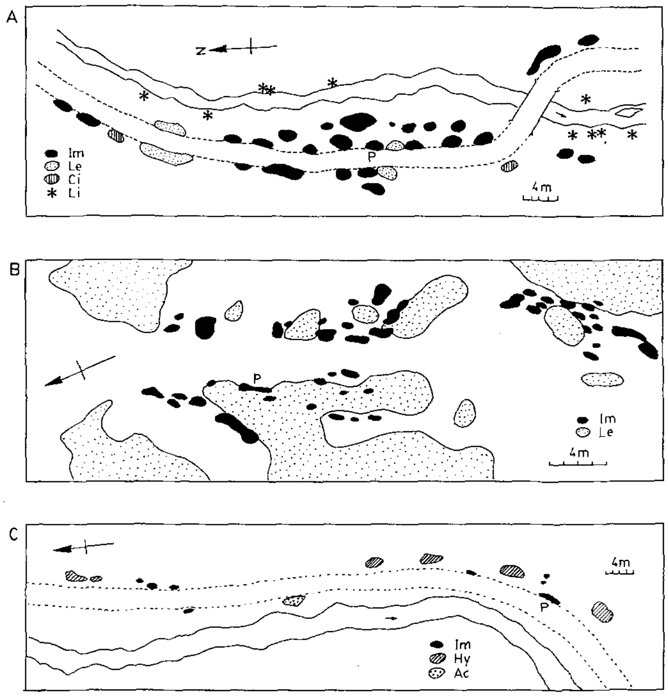

Fig. 1 A–C. Distribution of clumps of flowering plants: **A**, Observations T1–T4 at Kibune; *Im, Impatiens textori*; *Le, Leucosceptrum stellipilum*; *Ci, Cirsium microspicatum*; *Li, Liguraria fischeri*. **B**, Observation H1 at Mt Tsutsujo; *Im, Impatiens hypophylla*; *Le, Leucosceptrum stellipilum*. **C**, Observation N1 at Kibune; *Im, Impatiens noli-tangere*; *Hy, Hydrangea macrophylla*; *Ac, Actinidia arguta*. *P* indicates the patch studied

which bumblebees visited the patch, the trajectories of their flights among the flowers, and the duration of stay on each flower. I also recorded visits of other pollinators to flowers in the patch, although they were rare. Observations continued from sunrise to sunset, except for T1 and T2 when I arrived about an hour after sunrise.

The time of a bumblebee's visit to a flower was estimated from the time of its arrival in the patch and cummulative time spent on previous flowers and in inter-flower movements. From the temporal record of bumblebee visits to each flower, I estimated the time for which a flower had been unvisited, and hence the volume of nectar left in each flower.

Results

Flowering biology of Impatiens textori

The buds of *Impatiens textori* were usually first opened by foraging bumblebees. Of buds of *I. textori*, 82% were opened in the morning and the others in the afternoon. The flower was in male phase in the first day and in female phase, with stigma projecting from the anther mass, the next day. Most flowers fell off on the second day; the life span of a flower was 1.77 days on average ($n = 44$, s.d. = 0.522)

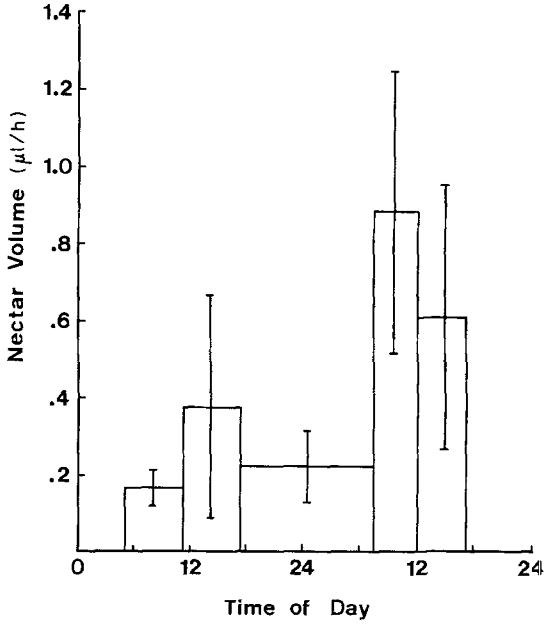

Fig. 2. Diurnal change in nectar secretion rate (µl/h) of *Impatiens textori*. *Bars*, standard deviation above and below the mean ($n = 10$)

I. textori flowers continuously secreted nectar throughout the 2-day flowering period. Figure 2 shows the changes in mean nectar-secretion rate in *I. textori*. The concentration of sucrose in the nectar was 35% on the first day and 17% on the next day. The nectar secretion rate in weight of sucrose per flower per hour in daytime (mean = 0.147 µg, $n = 30$) was higher than at night (mean = 0.038, $n = 10$), which is statistically significant ($t = 6.28$; $p < 0.01$). The mean amount of nectar secreted per flower throughout the blooming period was 13.4 µl ($n = 10$, s.d. = 3.9) in volume, and 2.64 µg ($n = 10$, s.d. = 0.94) in weight of sucrose.

Diurnal pattern of bumblebee visits

Flowers of *Impatiens* spp. were legitimately visited only by long-tongued insects, mostly bumblebees and a few sphingid hawk moths (*Macroglossum* spp.). The bumblebees that visited *Impatiens* spp. were exclusively *Bombus diversus* workers, most of which were mainly feeding on *Impatiens*. At observations T1–T4, most individuals of another bumblebee species, *B. honshuensis* were mainly feeding on *Liguraria fischeri*, and none visited *I. textori*. At H1, *B. diversus* was the only bee species foraging for flowers. At N1, most individuals of *B. hypocrita* and *B. honshuensis* were mainly feeding on *Hydrangea macrophylla* and *Actinidia arguta*, and none visited *I. noli-tangere*.

Figure 3 shows the pattern over the day of the number of bumblebee visits to flowers in a patch per hour at T1–T4 and H1. Bumblebees foraged for *Impatiens* flowers from just after sunrise to just after sunset. The number of bumblebee visits in a patch per hour in daytime ranged from 20 to 40, and was greater than in the early morning.

Table 2 summarises bumblebee visits to *Impatiens* spp. *I. textori* and *I. hypophylla* had more bumblebee visits than *I. noli-tangere* ($t=8.05$, $t<0.01$; $t=5.17$, $t<0.01$, respectively). The frequency of bumblebee visits may reflect the number of *B. diversus* workers in their colonies, which increased till September.

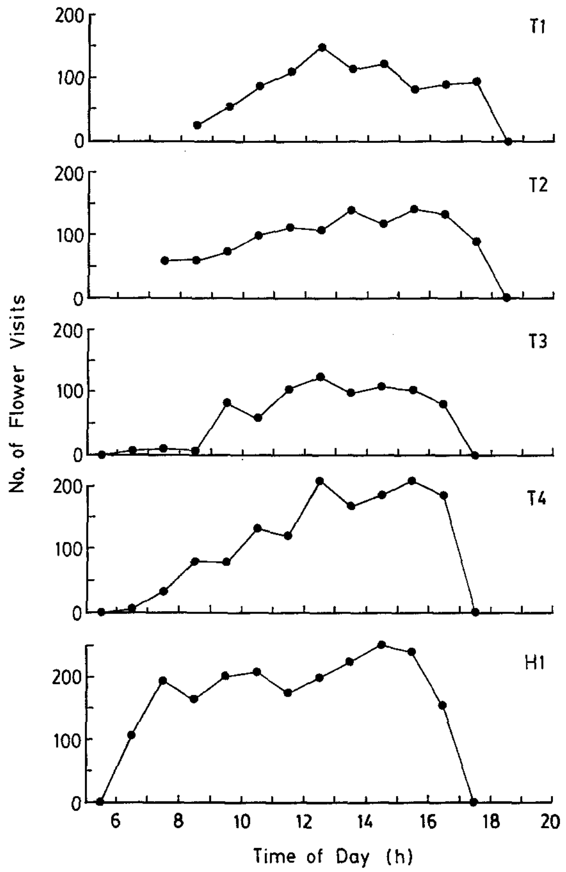

Fig. 3. Diurnal changes in the number of bumblebee visits on *Impatiens* flowers in a patch, observations T1–T4 and H1

There was variation in the number of bumblebee visits per day among individual flowers (Fig. 4). The percentages of *Impatiens* flowers with more than 10 bumblebee visits per day at T1–T4, H1, and N1 were 100%, 100%, 82.6%, 78.3%, 78.3%, and 10.0%, respectively.

Behavior on flowers

Bumblebees landed on the labiate corolla of *Impatiens* and protruded their long tongues into the spur to imbibe the nectar. Figure 5 shows the frequency distribution of the time spent on a flower for T1–T4 and H1. The mean time spent on individual flowers of *I. textori, I. hypophylla*, and *I. noli-tangere* was 3.14±2.20 min, 2.04±1.06 min, and 2.18±0.79 min (mean±s.d.), respectively. If time spent on a flower is less than 2 sec, bumblebees may not imbibe the nectar in the spur.

Figure 6 shows the relationship between the time spent on a flower and the time period for which the flower had

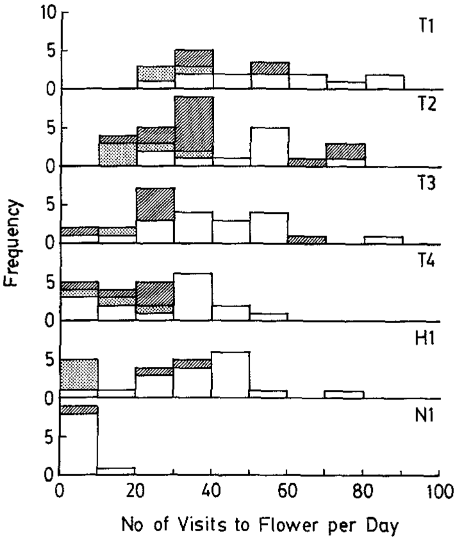

Fig. 4. Frequency distributions of the total number of bumblebee visits per flower in a day for observations T1–T4, H1, and N1. *Shaded, dotted*, and *open columns* refer to the flowers that fell off in daytime, those that opened after 1000 h and those that opened before 1000 h respectively

Table 2. Summary of bumblebee visits in a patch

Observation code	Total number of bumblebee visits in the patch per day	Mean number of bumblebee visits in the patch per hour	Total number of bumblebee visits to flowers in the patch per day	Mean±s.d. number of bumblebee visits to flowers per hour	Mean±s.d. length of stay on a flower (sec)	Mean number (%) of flowers visited per foraging trip in the patch
T1	261	29.6	934	5.87±1.81	3.27±2.65	3.58 (19.9%)
T2	330	31.1	1052	4.79±2.02	3.19±2.17	3.19 (11.0%)
T3	283	31.3	691	4.14±1.82	3.52±2.88	2.44 (10.6%)
T4	209	24.3	576	3.15±1.83	2.58±1.12	2.76 (12.0%)
H1	218	27.6	998	4.13±1.52	2.04±1.06	4.58 (17.0%)
N1	18	2.1	23	0.24±0.25	2.18±0.79	1.28 (11.6%)

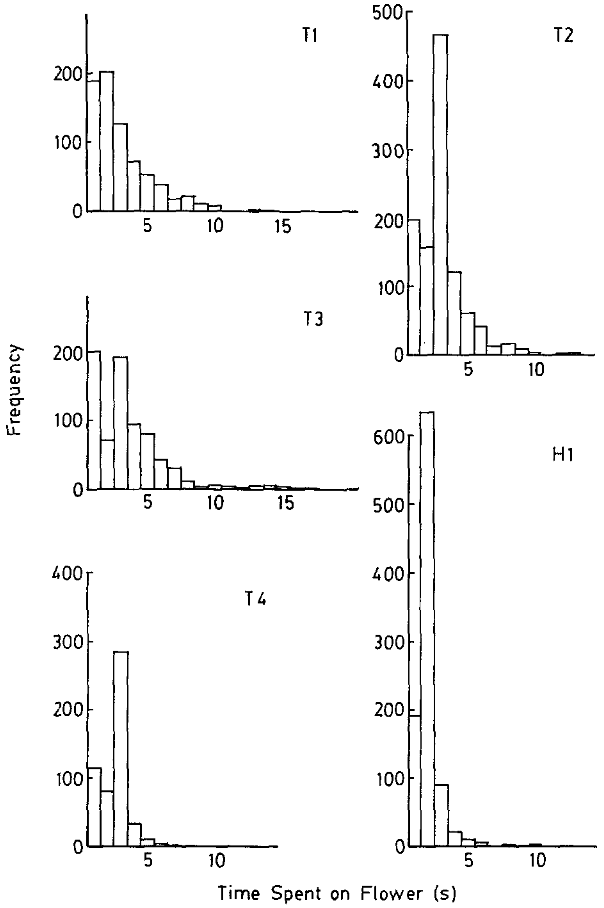

Fig. 5. Frequency distributions of the time (sec) spent on a flower by a bumblebee, for observations T1–T4 and H1

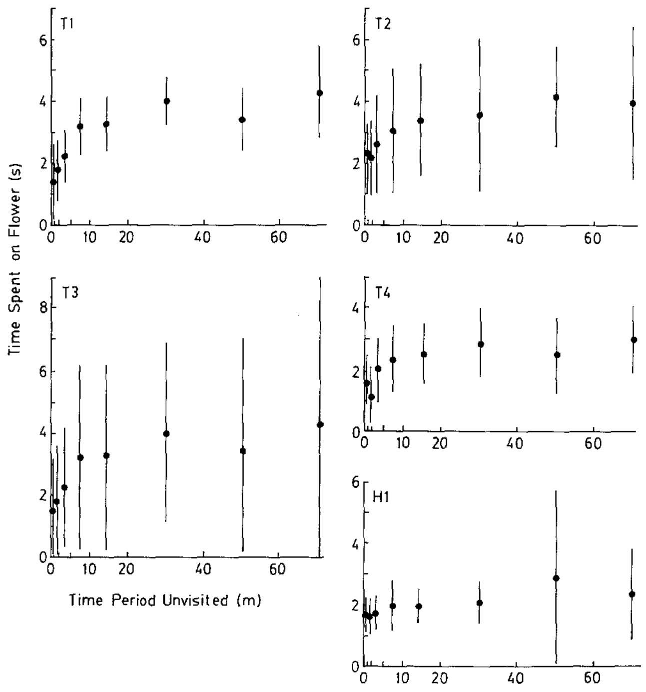

Fig. 6. Relationship between the time (sec) spent on a flower and the time period (min) for which the flower had been unvisited since the last visit, for observations T1–T4 and H1. The time period unvisited was grouped as follows: 0–1, 1–2, 2–5, 5–10, 10–20, 40–60, >60 min. *Bars*, standard deviations

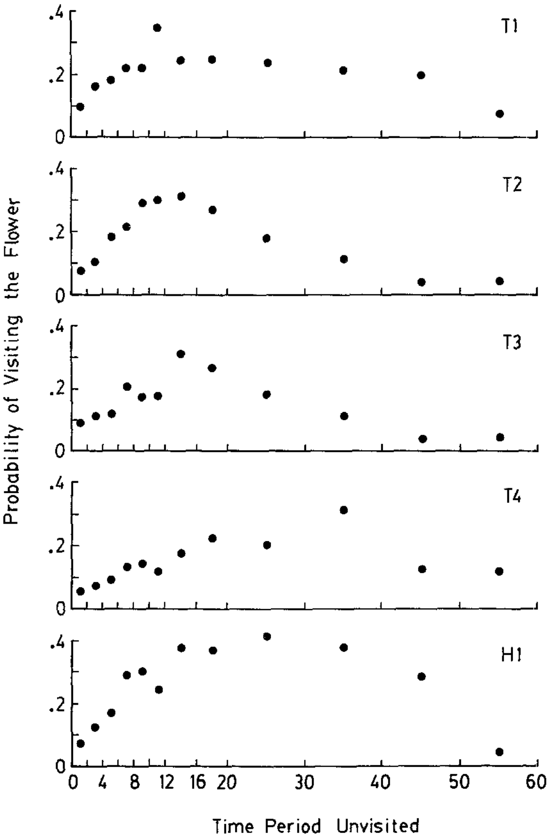

Fig. 7. Relationship between the time for which a flower has been unvisited since the last visit and the probability that a bumblebee entering the patch visits that flower, for observations T1–T4 and H1. The time period unvisited is grouped as follows: 0–2, 2–4, 4–6, 6–8, 8–10, 10–12, 12–16, 16–20, 20–30, 30–40, 40–50, >50 min

been unvisited since the last visit. The time unvisited is presumed to correspond to the volume of nectar, because *Impatiens* flowers secreted nectar continuously at a constant rate. The time spent on a flower which had been unvisited for less than 5 min was significantly shorter than on flowers unvisited for longer (T1, $t=8.08$, $p<0.001$; T2, $t=5.73$, $p<0.001$; T3, $t=7.24$, $p<0.001$; T4, $t=7.49$, $p<0.001$; H1, $t=7.71$, $p<0.001$). Figure 6 suggests that when a bumblebee visited a flower that had been visited recently by another individual, it often left the flower immediately.

Flower choice

A bumblebee flying into a patch of flowers might decide which individual flower to visit. I assumed that a bumblebee entering a patch can potentially choose any of all the flowers in a patch. Combining the records of bumblebee visits for each flower, I estimated the probability that a flower which had been unvisited for a certain time period would be visited by a bumblebee at its first visit in the patch. Then, I examined the relationship between the time period for which a flower had been unvisited since the last visit and the probability that a bumblebee entering the patch would visit that flower. The domed curve of this probability (Fig. 7) suggests that bumblebees avoided visiting a flower that (1) had been visited by another individual recently, and (2) had been unvisited by another individual for a long time.

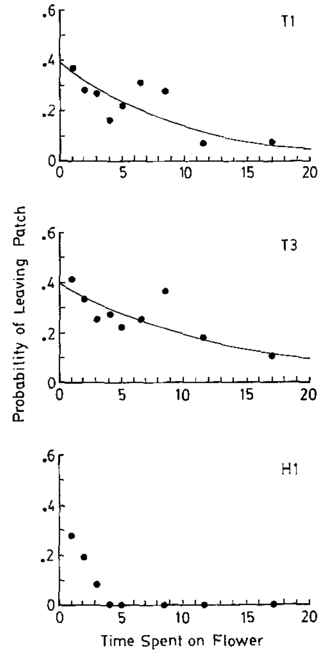

Fig. 8. The relationship between the time spent on a flower (sec) and the probability that a bumblebee would then leave the patch, for observations T1–T4 and H1. The time spent on a flower was grouped as follows: 1, 2, 3, 4, 5, 6–7, 8–9, 10–13, >14 sec

The decision to leave a patch

Combining the records of bumblebees leaving the patches, I estimated the probability that a bumblebee would leave a patch after visiting a flower where it had spent a certain time period. Then I examined the relationship between the time spent on a flower and the probability that a bumblebee would leave the patch. Figure 8 suggests that a bumblebee would have a higher probability of leaving a patch when it had stayed on a flower for a shorter time. The probability of a bumblebee leaving the patch decreased sharply over the first 3 sec spent on a flower. These data suggest that either nectar volume or a certain substance left on a flower might contribute to the bees' decision to leave a patch.

Figure 9 shows the frequency distribution of the number of flowers that a bumblebee visited in a foraging trip in a patch. The mean numbers of visit to flowers per trip for T1–T4, H1, and N1 were 3.58, 3.19, 2.44, 2.76, 4.58 and 1.28, respectively; the percentage of flowers visited out of the total number of flowers ranged from 10.6% to 19.9%.

Efficiency in nectar gathering behavior

Assuming that *Impatiens* flowers secreted nectar at a constant rate during daytime, that no nocturnal foragers had visited flowers in the night, and that a bumblebee visiting a flower depleted floral nectar, I estimated the amounts of nectar which the flowers contained. For example, Fig. 10 shows the diurnal fluctuations in the amounts of nectar (represented as weight of sucrose: μg) for 29 flowers at T2. The amount of nectar per flower changed sharply and continuously in response to the temporal pattern of bumblebee visits.

Then I calculated the mean amounts of nectar that an actual bumblebee and a hypothetical random forager could gather from a flower in the patch (Table 3). Here, I assumed

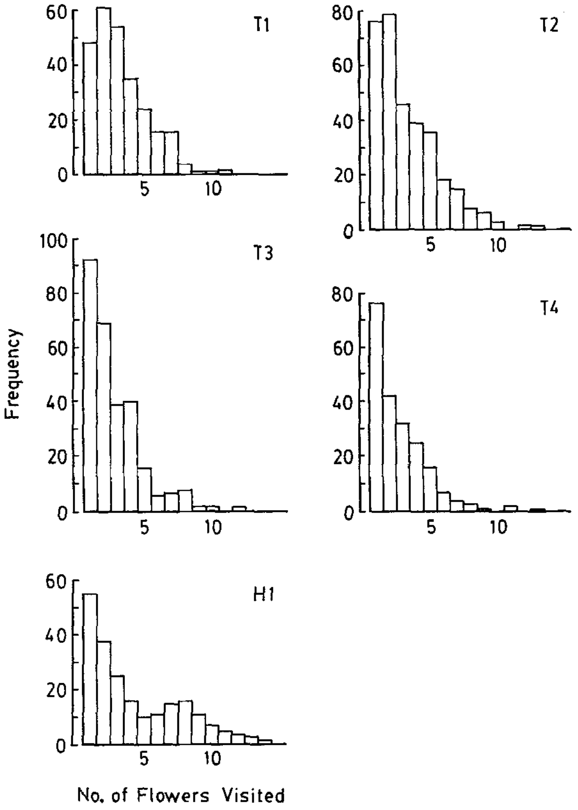

Fig. 9. Frequency distributions of the number of flowers that a bumblebee visited during a foraging trip in a patch, for observations T1–T4 and H1

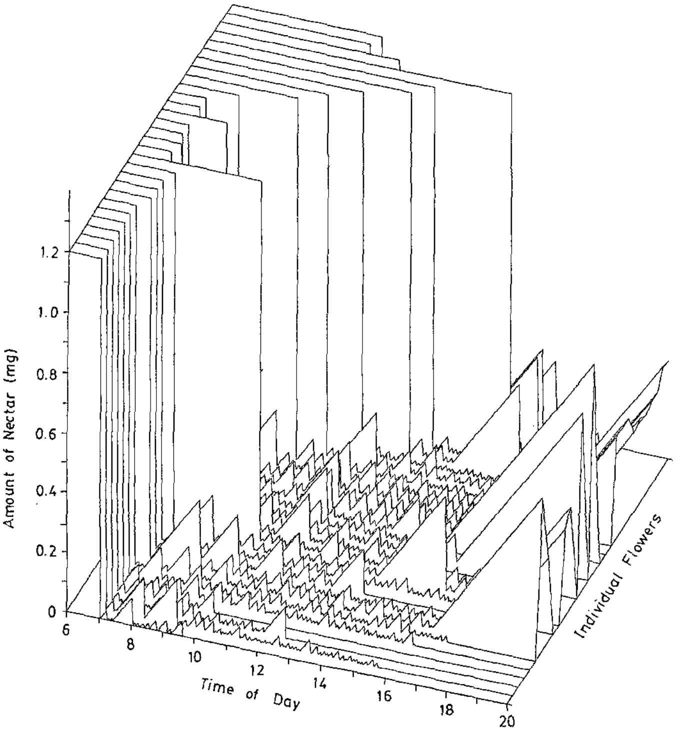

Fig. 10. Diurnal changes in the amount of nectar (represented as weight of sucrose: μg) for 29 flowers at T2

Table 3. Comparisons of nectar intake per flower per individual (sucrose weight: 10^{-2} mg) between the hypothetical bumblebee foraging randomly on flowers and the actual bumblebee

Observation code	Nectar intake per flower per individual	
	Hypothetical bumblebee Mean ± s.d. (Samples)	Actual bumblebee Mean ± s.d. (Samples)
T1	3.72 ± 7.27 (4752)	6.01 ± 17.11 (264)
T2	5.83 ± 9.86 (9570)	6.93 ± 19.74 (330)
T3	5.79 ± 9.81 (6792)	7.47 ± 22.16 (283)
T4	6.65 ± 12.08 (4807)	11.68 ± 22.16 (209)
H1	8.51 ± 19.68 (5886)	8.10 ± 23.93 (210)

that the random forager had the same pattern of visits in the patch as actual bumblebees, but made no flower choices and visited all flowers in the patch. For H1, I assumed that the rate of nectar secretion of *I. hypophylla* is the same as that of *I. textori.* Table 3 suggests that the mean amount of nectar gathered by an acutal bumblebee on an *I. textori* flower was significantly higher than the mean amount of nectar gathered by a hypothetical random forager. This result suggests that the bumblebees gathered floral nectar more efficiently than hypothetical random foragers.

Discussion

The three Japanese species of *Impatiens* were visited frequently by a long-tongued bumblebee species, *Bombus diversus.* Nectar robbers biting the spur, as reported by Rust (1977, 1979), were not observed. Though I could not observe visitors at night, *Impatiens* flowers might have been visited by nocturnal foragers such as hawk moths. Continuous nectar secretion by *Impatiens* at night and the low frequency of bumblebee visitors in early morning may suggest the presence of nocturnal visitors.

The high frequency of bumblebee visits in daytime in September assured pollination of *I. textori* flowers, which bloomed for only 2 days. The life span of *I. hypophylla* flowers was longer, though they were visited by bumblebees as frequently as *I. textori* flowers. Since the habitat of *I. hypophylla* along valleys in the southern part of Japan had high rainfall, it had to bloom longer to assure pollination. As an additional protection against rain, individual flowers of *I. hypophylla* bloomed beneath a sheltering leaf. *I. noli-tangere* flowers blooming in July were visited far less frequently than the other two species. *I. noli-tangere* flowers blooming in September, however, seemed to be visited more frequently than in July.

B. diversus workers showed three characteristic patterns of behavior in flower use, flower choice, and patch departure. First, bumblebees stayed on flowers that had been unvisited for a while for a longer time than on flowers that had been visited recently. Though the length of stay on a flower was not correlated with the time that flower had been unvisited, bumblebees immediately left flowers that had been visited less than 2 min previously. This suggests that bumblebees determined their length of stay not by checking the amount of nectar left in a flower but by perception of some chemical cue recently deposited by other individuals.

Second, bumblebees preferred visiting flowers which had been unvisited for a while to visiting those which had been visited recently, and to visiting those which had been unvisited for a long period (more than about 30 min). These results suggest that *B. diversus* worker could remotely perceive some cue that indicated how long the flower had been unvisited. Marden (1984) showed in the laboratory bumblebees approached and avoided non-rewarding flowers by remote perception of subtle visual or olfactory cues. The results of the present study could be explained if the cues which were remotely perceived by bumblebees were not direct signals of nectar volume (as suggested in Marden's study) but that some volatile substance was deposited on flowers by foraging bumblebees and disappeared gradually.

The tendency of bumblebees to reject flowers that had been unvisited for a long time was another characteristics of their pattern of flower choice. The flowers that had been unvisited for a long time appeared to be non-rewarding flowers due to small size or morphological flaws or other unknown reasons. Accordingly, this behavior implies another mechanism of remote perception. Cameron (1981) reported that foraging bumblebees deposited a substance on rewarding flowers which assisted in discrimination between rewarding and non-rewarding flowers in a controlled laboratory environment. The absence of the marking substance may be the cue by which *B. diversus* workers reject non-rewarding flowers without landing on them.

Third, a bumblebee had a higher probability of leaving a patch after it had stayed on a flower for a short period than after it had stayed for longer. Though the length of stay on the flower was not related to the time the flower had been unvisited, it can be regarded as a rough index of the amount of nectar left in a flower. Figure 8 suggests that bumblebees decided to leave a patch in response to some cue indicating the nectar reward of each flower.

Did these behaviors of *B. diversus* workers correspond to the optimal foraging strategy? The mean rate of nectar intake from *I. textori* flowers was 1.18–1.76 times higher than the mean amount of nectar left in the flowers. Thus, while the amount of nectar in each flower changed intermittently as a function of nectar secretion and bumblebee visits, *B. diversus* workers foraged for *I. textori* flowers more efficiently than hypothetical random foragers. To examine the optimality of their foraging behavior, it will be necessary to incorporate complex cost-benefit functions for bumblebee foraging and spatial distribution of patches and flowers. I can only conclude that a gene for random foraging could not invade a population of actual *B. diversus* workers which forages for *Impatiens* flowers in the manner indicated by this study.

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