Naturwissenschaften (2013) 100:659–666
DOI 10.1007/s00114-013-1062-1

ORIGINAL PAPER

Longer visits on familiar plants?: testing a regular visitor's tendency to probe more flowers than occasional visitors

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Received: 11 March 2013 / Revised: 20 April 2013 / Accepted: 17 May 2013 / Published online: 21 June 2013

Abstract An individual pollinator may tend to consecutively probe more flowers on a plant to which it returns at shorter intervals than other plants. In a large net cage, I let individually marked bumble bees forage on flowering heads of red clovers arranged in 37 bottles (plants), each of which was monitored by an observer to record every visit and probe for 2.5 h on each of 3 days. The data of collective visits by marked individuals revealed that the bees had their own foraging areas, in which they visited a set of plants frequently and others less often, i.e., the same individual bee repeatedly returned to certain plants as a regular visitor while sampling others as an occasional visitor. I further found that as a regular visitor, an individual bee tended to probe more flowering heads on familiar plants while probing fewer on unfamiliar plants as an occasional visitor. The mean number of consecutive probes by a bee was also positively correlated with its activity (the total number of plant visits made during the observation period). The fact that each bee behaves differently on different plants indicates that the same individual pollinator can exert different influence on the reproductive success of each plant: apparently, a pollinator likely reduces the potential for geitonogamous self-pollination when foraging as an occasional visitor. Attracting occasional visitors therefore may be beneficial for plants to avoid geitonogamy. This study thus emphasizes the importance of paying attention to pollinator individuality in pollination ecology.

Keywords *Bombus ignitus* · Foraging area size · Geitonogamy · Individual visitation rates · Plant–pollinator interaction

Communicated by: Beverley Glover

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Introduction

A pollinator consecutively probing flowers on a plant is an important determinant of plant reproduction because the inter-flower movement increases the opportunity for geitonogamous self-pollination: as a pollinator probes more flowers on a plant, more self-pollen moves among flowers (Karron et al. 2004). Geitonogamy can reduce a plant's mating success by using pollen that could otherwise have been exported to other plants (Harder and Barrett 1995) and, in self-compatible species, by reducing both the production of outcrossed seeds and offspring performance due to inbreeding depression (Lloyd 1992). Therefore, factors affecting successive probes merit study.

The number of successive flower probes by pollinators is known to vary depending on various factors. A pollinator probes more flowers (or flowering heads) on a plant, for example, in a sparse plant population (Ishii et al. 2008; Ohashi and Yahara 2002), without competitive foragers (Makino and Sakai 2005), with simple flowers (Ohashi 2002), smaller flowers (Ishii and Harder 2006), higher rewards (Cresswell 1990; Hodges 1985; Thomson et al. 1982), less variable rewards (Biernaskie et al. 2002; Pappers et al. 1999), and many flowers (Harder and Barrett 1995; Grindeland et al. 2005; Karron et al. 2004; Mitchell et al. 2004; Miyake and Sakai 2005; Ohashi and Yahara 1998, 2002; Robertson and Macnair 1995; Vrieling et al. 1999). All of these patterns have implications for the direction of selection exerting on floral traits such as display size, flower shape, nectar secretion rates, and inflorescence architecture, among others.

The number of successive flower probes may also vary with pollinator individuality, as suggested by Williams and Thomson (1998). By putting identification marks on bumble bees and recording their respective visitation rates to a single plant, they revealed considerable variation among bees in visitation rates, i.e., the plant was visited by a couple of “regular visitors” (bees that made frequent returns) and many “occasional visitors” (bees that visited the plant less often). Moreover, they found that regular visitors tended to probe more flowers per plant visit than occasional visitors, indicating that pollen grains removed by regular visitors are more likely to be used in geitonogamous selfing. However, the correlation was found only at the single plant on a single day, and to date, no one has tested it in other systems despite the possible effect on plant reproduction.

It also remains unclear how a regular visitor to a plant behaves on other plants (e.g., whether it acts as a regular or occasional visitor). There are several possibilities. (1) A regular visitor to a plant is likely to be an active forager in a plant population and probe many flowers on other plants as a regular visitor, too. (2) A regular visitor to a plant may act differently on other plants. Individual pollinators, such as bumble bees and hummingbirds, often confine their foraging to small areas within a larger plant population (Comba 1999; Gill 1988; Heinrich 1976; Thomson et al. 1982, 1987), and within their own foraging areas, individual pollinators can visit particular sets of plants more frequently than other plants (Makino and Sakai 2004, 2005; Thomson et al. 1997). This means that a regular visitor to a plant can be occasional to another plant on which it may probe fewer flowers. (3) More probes by regular visitors might reflect exploitative defense by pollinators foraging in small areas. In Makino et al. (2007), while some bees searched large areas in a plant population, visiting many plants as occasional visitors, others showed very small foraging areas, repeatedly returning to a limited number of plants as regular visitors. To defend their own areas, such pollinators with small foraging areas may deplete more flowers than those searching larger areas. The number of successive probes by a pollinator may therefore negatively correlate with its foraging area size. Examining these possibilities will help us to consider the role of individual pollinator foraging strategies to successful plant reproduction. For example, if large area searchers tend to probe fewer flowers on a plant, it would be beneficial for plants to attract such visitors to increase the level of outcrossing and reduce potential inbreeding.

To address these questions, *Bombus ignitus* (bumble bees) foraging on *Trifolium pratense* (red clovers) were observed in a large net cage. In this cage, flowering heads of red clover were arranged in 37 bottles (hereafter, “plants”) to make a plant population with a uniform distribution of floral resources. By taking advantage of teaching a plant ecology class, I let 37 students record every visit and probe made by individually marked bees to plants in the cage on 3 days (2.5 h a day). Based on the results from the large data sets (277.5 h in total), I discuss the possible effects of pollinator individuality on plant reproduction and suggest directions for future studies.

Materials and methods

Bumble bees (*B. ignitus*, Hymenoptera) foraging on red clover (*T. pratense*, Fabaceae) were observed on 3 days (2 June 2003, 5 June 2003, and 9 June 2004, hereafter days 1, 2, and 3), in a 20.0×20.0-m net cage with a height of 2.0 m, placed outside in a grassland habitat in Sanjo, Sendai, Japan. The net mesh size (6.0 mm) was fine enough to prevent the bees from going outside and exclude flower visitors from the outside. The other flowering plants in the cage were completely mowed.

Two commercial colonies of bumble bees (supplied by Arysta LifeScience, Japan) were used, each of which was set in a corner of the cage in each year (Fig. 1). To identify individual bees, I numbered all of the workers by gluing tags to their thoraxes. As an index of body size, I measured their forewing length from where it attached to the thorax to the tip of the wing.

One hour prior to the start of observations each day, flowering heads of red clovers growing around the cage were collected and arranged vertically in 37 plastic bottles with wires (Fig. 2). The 37 “plants” were placed on tables arranged in a hexagonal array (Fig. 1) according to Thomson et al. (1997). The height of a table (70 cm) allowed observers sitting in front to monitor bee visits without disturbing their inter-plant movements (i.e., bees flew over the observers’ heads). All distances between neighboring plants were equivalent in the array (2.0 m), which reduced the effects of variation in inter-plant distance on bee visitation (Thomson et al. 1997). To remove the effect of variation in flower head number per plant on the number of successive probes, each plant had the same number of flowering heads (four in 2003 and six in 2004), constituting a uniform distribution of floral resources in the cage.

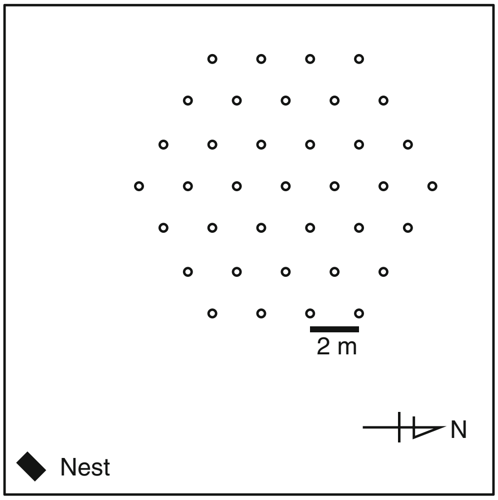

Fig. 1 A schematic of the top view of the net cage with the red clover array. *Small circles* indicate bottled plants

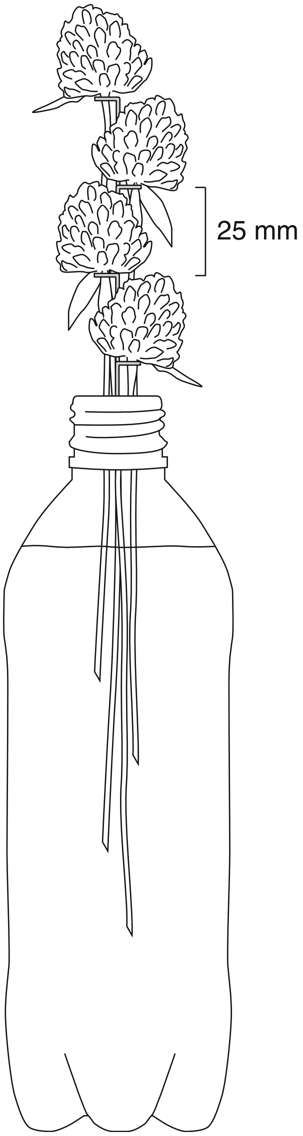

Fig. 2 A schematic of the red clover flowering heads vertically arranged in a plastic bottle used as "plants" in this study

The gate of a nest was opened about 1 h before the observation of each day to allow bees to freely forage on red clovers and closed after the observation (the bees could then enter the nest but not exit due to a non-return valve). I also let the bees out for about 4 h on 2 June 2003 and 2 June 2004, prior to the observation, to give the bees experience with foraging on red clover flowers. The bees foraged in a population of red clovers with a heterogeneous flower distribution on 3 and 4 June 2003 and 3 and 7 June 2004 for another purpose (Makino TT, in preparation). Although the bees collected both nectar and pollen from red clover, they seemed to mainly forage for nectar, as all bees inserted their tongues into the florets and their pollen loads seemed to passively accumulate through grooming. I supplied pollen ad lib every evening, directly to the colony.

To record every visit and probe made by individual bees in the cage, 37 students observed a plant each. Each student recorded the identification of individual visitors to their assigned plant and the number of flowering heads probed by each visitor for 1330–1615, with a 15-min break in the middle (i.e., 2.5 h per day). Students were shuffled among plants during the break.

Analysis

I used Kendall's rank correlation analysis with a blocking variable (Korn 1984) to test whether the number of visits to a plant by a bee correlated with the mean number of heads probed by the bee on the plant within an observation day, considering individual bees or plants as a blocking variable. To calculate Kendall's blocked tau (τ_{blocked}), normal Kendall's tau (τ) was computed for each block. When treating individual bees as a blocking variable, I used bees that visited at least two different plants because τ cannot be calculated for a bee that visited only a single plant. The number of bees observed at multiple plants was 23, 26, and 41 on days 1, 2, and 3. On the other hand, in the calculation of τ_{blocked} with individual plants as a blocking variable, the bees seen only at a single plant were included together with those observed at multiple plants. I used the same analysis to test whether the mean number of heads probed per plant visit by a bee (total number of heads probed/total number of plant visits) correlated with the bee's (1) foraging area size, (2) total number of plant visits (as an index of activity), and (3) forewing length (as an index of body size), with observation day as a blocking variable.

Evaluation of foraging area size

To evaluate the foraging area size of a bee on a day (the number of plants mainly used by the bee), counting the number of plant individuals visited by the bee was insufficient due to the heterogeneity of frequency distributions of visits to the plants and the variation in the number of plant visits among bees. To solve this problem, I used the rarefaction method (Hurlbert 1971; Simberloff 1972; cf. Krebs 1999) to evaluate foraging area size (see the same application in Makino and Sakai 2004, 2005). The rarefaction method determines $E(\hat{S}_n)$, the expected number of plant individuals visited if a bee makes n total plant visits, from its data set. The formula is as follows:

$$E\left(\hat{S}_n\right) = \sum_{i=1}^{S}\left[1-\frac{\binom{N-N_i}{n}}{\binom{N}{n}}\right],$$

where S is the total number of plant individuals visited by a bee, Ni is the number of visits to the ith plant, N is the total number of plant visits made by the bee, and $\binom{N}{n}$ is the number of combinations of n plant visits that can be chosen from the bee's data set consisting of N plant visits [equal to $N!/n!(N-n)!$]. In this study, I set $n=50$ and defined $E(\hat{S}_{50})$ as the foraging area size of a bee. Mean values are given with ±1 SD unless otherwise stated.

Results

The total number of individual bees seen in the red clover population on days 1, 2, and 3 was 32, 41, and 60, respectively. Those bees varied in the total number of plant visits made on a day (day 1, 27.6±35.3, range 1–116; day 2, 42.4±65.8, range 1–271; day 3, 46.1±62.7, range 1–205) and showed their own spatial foraging patterns (Fig. 3) with various foraging area sizes ($E(\hat{S}_{50})$, day 1, 27.2±1.44, $n=8$, range 25.0–28.5; day 2, 27.0±1.74, $n=10$, range 22.2–28.6; day 3, 24.5±2.72, $n=22$, range 16.9–28.7). Within their own foraging areas, individual bees visited a set of plants frequently and others less often (Fig. 3), i.e., a regular visitor to a plant became an occasional visitor to another plant.

From the viewpoint of plants, regular visitors tended to probe more flowers than occasional visitors: with individual plants as a blocking variable, there were positive correlations between the number of visits to a plant by a bee and the mean number of heads probed per visit by the bee [Fig. 4; day 1, $\tau_{\text{blocked}}=0.0930$, $P=0.0049$, $n=419$ (37 plants); day 2: $\tau_{\text{blocked}}=0.0505$, $P=0.0896$, $n=550$ (37 plants); day 3: $\tau_{\text{blocked}}=0.111$, $P=0.0006$, $n=804$ (37 plants)]. Those correlations were still significant when individual bees were treated as a blocking variable instead [Fig. 4; day 1: $\tau_{\text{blocked}}=0.0792$, $P=0.0114$, $n=410$ (23 bees); day 2: $\tau_{\text{blocked}}=0.0945$, $P=0.0007$, $n=535$ (26 bees); day 3: $\tau_{\text{blocked}}=0.131$, $P<0.0001$, $n=785$ (41 bees)]. This means that the same individual bee tended to behave differently on different plants, probing more flowering heads on familiar plants while fewer on less familiar plants.

With days as a blocking variable, the mean number of heads probed per visit by a bee significantly increased with the total number of plant visits by the bee [Fig. 5; $\tau_{\text{blocked}}=0.130$, $P=0.0262$, $n=133$ (32, 41, 60 bees each day)], i.e., active foragers tended to probe more heads per plant visit than less active foragers. In contrast, the mean number of probes by a bee neither varied with its foraging area size [$\tau_{\text{blocked}}=-0.00356$, $P=0.953$, $n=30$ (8, 10, 22 bees each day)], nor with its forewing length [$\tau_{\text{blocked}}=0.0309$, $P=0.619$, $n=123$ (32, 39, 52 bees each day)]. Furthermore, forewing length of a bee neither correlated with its foraging area size [$\tau_{\text{blocked}}=0.0125$, $P=0.842$, $n=38$ (8, 10, 20 bees each day)], nor with the number of total visits [$\tau_{\text{blocked}}=0.0825$, $P=0.179$, $n=123$ (32, 39, 52 bees each day)].

Discussion

As Williams and Thomson (1998) detected at the single *Penstemon strictus* plant, I also found the positive correlation between the mean number of probes by a bumble bee on a plant and its visitation rate to the plant (Fig. 4), i.e., in the present study, regular visitors tended to probe more flowering heads on familiar plants, too. Thus, this pattern may be more general.

Furthermore, the present study revealed that the pattern resulted from within-bee variation across different plants. That is, as indicated by the significant correlations with individual bees as a blocking variable, an individual bee

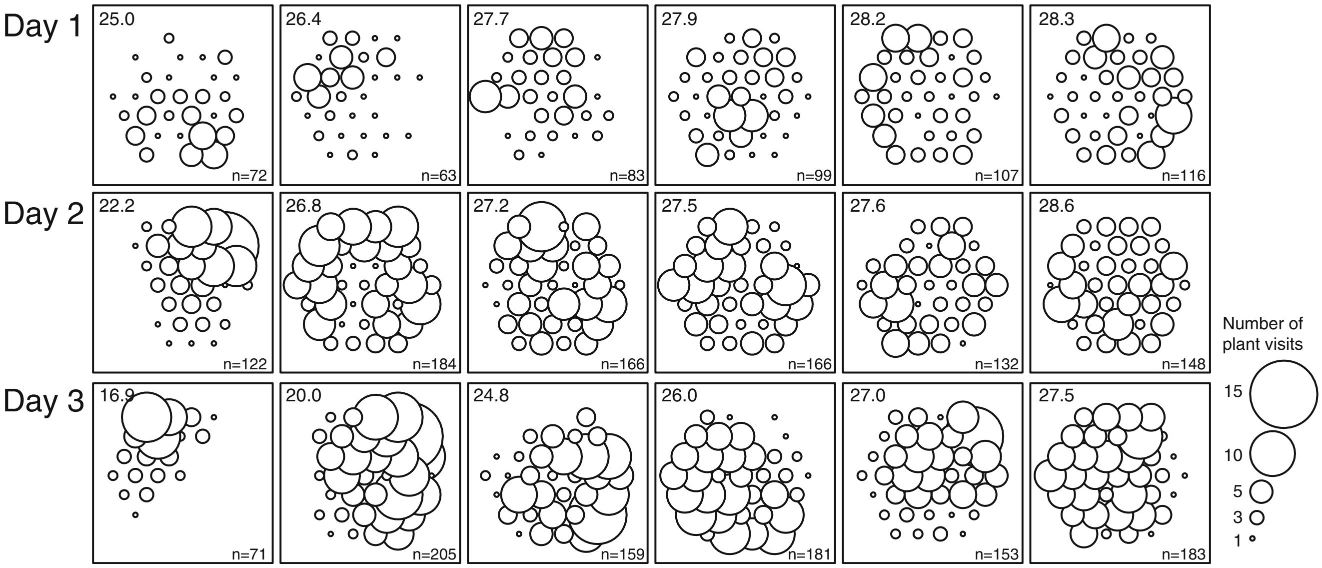

Fig. 3 Examples of spatial foraging patterns of different bee individuals in the red clover array. The size of a circle indicates the number of visits to that plant. The size of the foraging area [$E(\hat{S}_{50})$] and the number of plant visits (n) are shown in the *upper left* and *lower right corners of each panel*, respectively

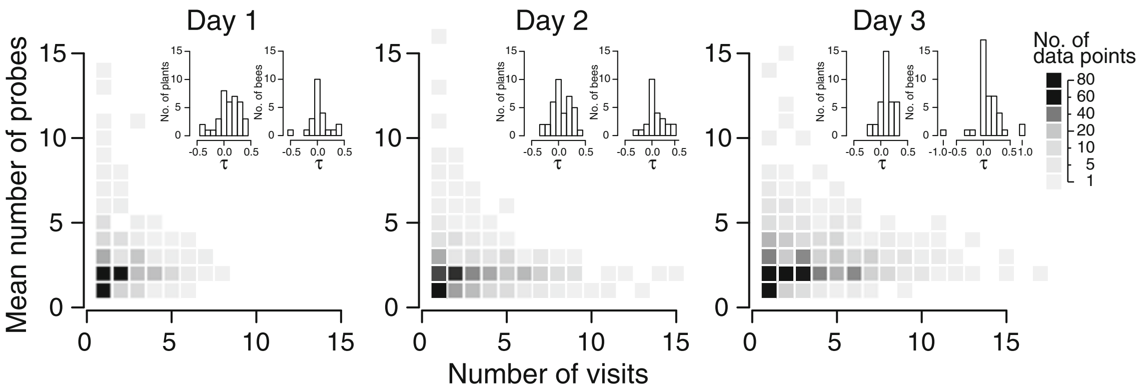

Fig. 4 Scatter plots of the number of visits to a plant versus the mean number of flower probes on the plant. The *gray scale* indicates the number of data points. n=419, 550, and 804 on days 1, 2, and 3, respectively. Embedded histograms show the distributions of Kendall's τ used to calculate τ_{blocked} with plants (*left*) or bees (*right*) as a blocking variable

tended to probe more flowering heads on familiar plants while fewer on less familiar plants. The fact that an individual forager behaves differently on different plants means that the same individual pollinator can exert different influence on plant reproductive success.

I also found that more active foragers tended to probe more flowering heads per plant visit than inactive ones (Fig. 5), indicating that the focal pattern resulted not only from within-bee variation across different plants, but also from among-bee variation in activeness. Although it was unclear whether inactive foragers were literally inactive (e.g., staying in their nests most of the time) or were actively searching for other floral resources instead of foraging on red clovers, they did not seem to contribute substantially to pollen transfer among conspecific plants. Plant fitness therefore might decrease with an increasing proportion of such inactive foragers.

Implications of "longer visits on familiar plants" for plant reproduction

Although it is suggested that regular visitors ensure more reliable visits (Makino et al. 2007), apparently, regular visitors more likely increase the potential for geitonogamous self-pollination than occasional visitors. Thus, it may be beneficial for both self-compatible and self-incompatible plant species to attract occasional visitors to increase the level of outcrossing and reduce potential inbreeding. Occasional visitors could possibly be (1) naïve foragers in search of profitable floral species (Heinrich 1979), (2) foragers that sample the focal species while majoring other floral species (Heinrich 1976), (3) foragers that major on the focal species but are unfamiliar with the plant individuals being considered (Makino et al. 2007; Thomson et al. 1982, 1997), or (4) intermittent foragers mainly engaging in other activities. Occasional visitors may respond differently to floral traits compared to regular visitors, opening up the possibility for selection to act on floral traits that increase visits by occasional pollinators. Makino and Sakai (2007) suggest that large floral displays attract such occasional visitors very well. Other floral traits for initial attraction such as conspicuous colors or remotely noticeable scents also seem to be effective in increasing the likelihood of visitation by occasional visitors. However, when occasional visitors are naïve foragers sampling various flowering species (Heinrich 1979), they could increase heterospecific pollen

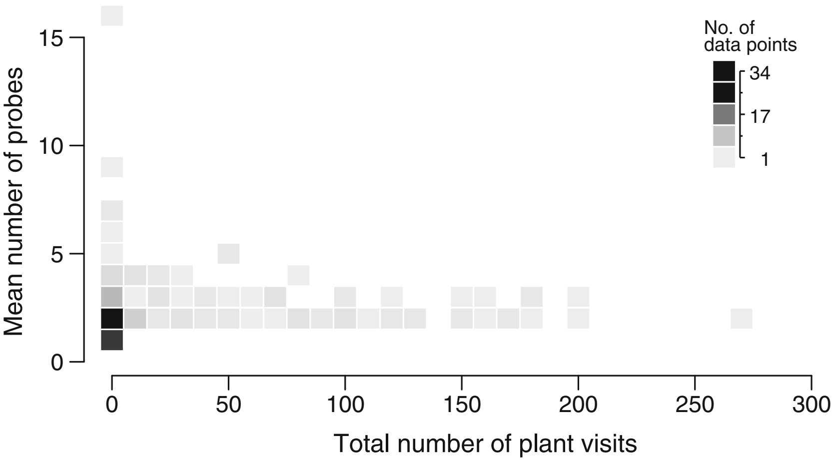

Fig. 5 A scatter plot of the total number of visits by a bee on a day versus the mean number of probes per plant visit by the bee. The *gray scale* indicates the number of data points. n= 133. Kendall's τ used to calculate τ_{blocked} is −0.022, 0.072, and 0.247 on days 1, 2, and 3, respectively

transfer, which may be detrimental for plant reproduction (Morales and Traveset 2008). Thus, some plants may face a trade-off between reducing geitonogamy and heterospecific pollination.

Causal relationship: frequent returns to profitable plants or defense by depletion?

I should note that there still remains an interesting question for future research: why do pollinators tend to probe more flowers on familiar plants? In general, they are known to probe more flowers on plants that have accumulated a large amount of resource (Cresswell 1990; Hodges 1985; Thomson et al. 1982). In addition, some pollinator species with good spatial memories prefer to return to such rewarding plants (Cartar 2004; Hurly 1996; Makino and Sakai 2007). In the present study, bees that happened to encounter relatively unexploited plants with accumulated rewards might be encouraged to revisit them and become regular visitors. Williams and Thomson (1998) reported that although regular visitors did not return to a plant when whole plant resource levels were higher, they did get greater rewards than occasional visitors by somehow selecting flowers with accumulated nectar, which suggests the presence of some beneficial information only available to regular visitors. Greater gains and frequent returns may set up a positive feedback loop, leading to the pattern found here. Another possibility is that a regular visitor may indirectly defend a plant from other foragers by reducing the whole plant resource level. In fact, traplining hummingbirds are known to shorten revisit intervals to plants when they detect depleted flowers, which is a sign of competitors (Garrison and Gass 1999; Gill 1988; Temeles et al. 2006). Although thorough depletion might not fit the prediction from the marginal value theorem (Charnov 1976), such exploitative defense of familiar plants (exclusive use by frequent returns and extensive probing in the present case) would ensure gains at future visits by making intruders leave earlier and discouraging them from revisiting the plants. Note that exploitative defense would also explain fewer probes by occasional visitors.

It should be noted that the focal pattern has occurred in populations with relatively higher visitation rates by abundant bees (Williams and Thomson 1998 and this study). Additionally, bees in those two populations showed small foraging areas (Thomson et al. 1997; Fig. 3), which suggests intense competition among bees (Makino and Sakai 2005). If the presence of competitors elicits extensive probing as discussed above, foragers may not show the focal pattern when there’s no need to defend plants, for example, in a population with a few individual pollinators. Field researches in less competitive populations, or experiments in a closed system, which allows us to adjust the number of competitors, will answer this question.

Other pollinator taxa

Another important question is: how common is the pattern of longer visits to familiar plants among other pollinator taxa? To date, two species of bumble bees, *Bombus flavifrons* (Williams and Thomson 1998) and *B. ignitus*, in this study have been observed to stay longer on familiar plants (in addition, *Bombus diversus* showed the same trend on *Circium purpuratum*, T. T. Makino, unpublished data). The behavior therefore seems common among *Bombus* species. It might be also common among other pollinators, for example, birds, butterflies, and bats, some which are known to develop their own territories, returning to the same individual plants repeatedly (Gill and Wolf 1975; Lederhouse 1982; Lemke 1984; Linhart 1973; Murawski and Gilbert 1986; Paton and Carpenter 1984). On the other hand, due to the lack of research with identification of individuals, we know little about the site faithfulness of other major pollinator taxa including beetles and flies (Thomson and Chittka 2001; Weiss 2001). If these pollinators are just vagabonds and hardly become familiar with certain individual plants, there is no need for them to defend plants by exploitation. Flowering species depending on such vagabonds may receive fewer successive probes and experience less geitonogamous pollination.

Conclusion

The fact that individual pollinators behave differently on the same plant emphasizes the importance of paying attention to pollinator individuality when we study plant reproduction (Thomson and Chittka 2001). This study showed not only the positive correlation between the mean number of probes on a plant by a bee and the visitation rate to the plant (Fig. 4), but also that individual visitors had their own foraging areas that varied in size and included different sets of individual plants (Fig. 3). The among-bee variation in foraging area indicates that different visitors transfer pollen from different donors to different recipients. Although most previous studies have measured pollinator behavior without the identification of individual visitors, dissecting the collective data of anonymous pollinators into visits and probes made by identified individuals will further improve our understanding of the dynamics of pollen flow both within and among plants. Although the observation of individually marked visitors is laborious and technically difficult, especially for tiny or quickly moving pollinators, we clearly need more research on identified foragers across various pollinator taxa.

Acknowledgments I thank Jane Ogilvie for her helpful comments and editing my English in the original version of this manuscript, two anonymous reviewers for their valuable comments, Masahiro Mitsuhata in Arysta LifeScience for supplying bees, and the third year students in a biology course at Tohoku University in 2003 and 2004 for their extensive cooperation in the observation with great patience. I also thank the students in 2002 for their help to conduct a pilot observation. The experiments conducted for this study comply with current Japanese law.

Conflict of Interest The author declares no conflict of interest.

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