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INNATE OR LEARNED PREFERENCE FOR UPWARD-FACING FLOWERS?: IMPLICATIONS FOR THE COSTS OF PENDENT FLOWERS FROM EXPERIMENTS ON CAPTIVE BUMBLE BEES

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Abstract—Pollinator preferences for phenotypic characters, including floral orientation, can affect plant reproductive success. For example, hawkmoths and syrphid flies prefer upward- over downward-facing flowers in field experiments. Although such preferences suggest a cost of pendent flowers in terms of pollinator attraction, we cannot rule out the possibility that the preferences have been affected by prior experience: pollinators might choose the same type of flowers to which they have already become accustomed. To test for innate preference, we observed bumble bees foraging on an array of upward- and downward-facing artificial flowers. Without any prior experience with vertical flowers, 91.7% bees chose an upward-facing flower at the very first visit. In addition to this innate preference, we also found that the preference was strengthened by experience, which suggests that the bees learned upward-facing flowers were easier to handle. Although bumble bees may concentrate on pendent flowers in the field, such learned preferences are evidently imposed on a template of upward-facing preference. Because bee-pollinated pendent flowers face particular difficulties in attracting visits, therefore, we expect them to compensate through other means, such as greater floral rewards.

Keywords: Flower orientation, innate preference, learning, artificial flower, Bombus impatiens

INTRODUCTION

In animal-pollinated plants, the number of pollinator visits to a flower is an important determinant of reproductive success because more visits usually mean more pollen transfer (Galen & Stanton 1989; Wilson & Thomson 1991; Jones & Reithel 2001; Engel & Irwin 2003). Many studies on floral traits affecting pollinator visitation have revealed pollinator preferences, for example for larger flowers (Galen & Newport 1987; Johnson et al. 1995; Conner & Rush 1996; Morinaga & Sakai 2006), greater rewards (Pleasants 1981; Thomson 1988; Cartar 2004; Makino & Sakai 2007), and certain colours (Lunau & Maier 1995; Kelber 1997; Weiss 1997; Gumbert 2000), offering insight into the adaptive significance of various floral traits.

Flower orientation is one such trait affecting pollinator visitation. Manipulation of flower orientation has revealed hawkmoths' preference for upward- over downward-facing flowers of *Aquilegia pubescens* (Fulton & Hodges 1999), and syrphid flies' preference for upward-facing or horizontal flowers over downward-facing flowers of *Commelina communis* (Ushimaru & Hyodo 2005, Ushimaru et al. 2009). These findings suggest that a pendent orientation will intrinsically make a negative contribution to pollinator attraction, all else being equal. This would tend to increase the likelihood of pollen limitation or lower siring success, which in turn might select for countervailing characteristics, such as greater floral rewards in pendent flowers. On the other hand, no preference for flower orientation has been found in hummingbirds (Tadey & Aizen 2001; Castellanos et al. 2004). The different responses among pollinators have some implications for "pollination syndromes", in which flowers show a set of traits that correspond to a particular functional group of pollinators (Fenster et al. 2004). For example, the adaptive function of pendent flowers of the hummingbird-pollinated *Aquilegia formosa* (Fulton & Hodges 1999) may not be to match hummingbirds' preference, but rather to exclude hawkmoths.

Therefore, the role of flower orientation merits study, but we have to be cautious about interpreting observed preferences because we can not rule out the possibility that those preferences have been affected by prior experience, as pointed out by Ushimaru & Hyodo (2005). For example, the hawkmoths might choose upward-facing flowers just because they had already gotten accustomed to upward-facing flowers, and the syrphids might have had experience with upward-facing flowers of other species. To understand how the behavioural ecology of pollinators translates to selection on floral orientation, we wish to determine whether an observed preference is innate or learned; this requires controlling the prior experience of individual pollinators (Thomson & Chittka 2001).

To provide the first test on naïve insects, we performed lab experiments using artificial flowers and captive bumble bees, *Bombus impatiens*. Some bumble bees do specialize in

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flowers that face down (e.g., Kobayashi et al. 1997; Mahoro 2003), so that researchers tend to think that they do not have any preference against pendent flowers. Indeed, Huang et al. (2002) found no such preference by *Bombus* spp. foraging on *Pulsatilla cernua*, whereas the manipulation of flower orientation by Ushimaru & Hyodo (2005) showed that *Bombus diversus* preferred upward- to downward-facing flowers, though the preference was not statistically significant and might be biased by previous experience. Surprisingly, there are no other studies, and bumble bee preference for flower orientation remains unclear. In this study, we address two questions: 1) do *Bombus impatiens* workers show any preference for upward- or downward-facing flowers?; and 2) is the preference innate, or learned? Then we discuss the costs and benefits of pendent flowers.

MATERIALS AND METHODS

We used two commercial colonies of *Bombus impatiens* (supplied by Biobest, Leamington, Ontario, Canada). A colony was connected to a flight cage with a gated tunnel so that we could control entry of bees into a screen cage, 240 cm long x 220 cm wide x 220 cm high. The nest entrance was located at 100 cm height. We set a table (33 cm long x 55 cm wide x 90 cm high) 180 cm from the entrance, on which we placed artificial flowers.

We made artificial flowers by cutting 1ml pipette tips and mounting a pair of them to a length of styrene plastic tubing (stem) of 6 mm internal diameter, capped at one end (Fig. 1a). The narrow ends of the pipette tips were enlarged to provide a friction-fit over two small tubes that communicated with the interior of the stem. To provide bees with a better grip on flowers, we abraded both inside and outside of floral surfaces with sandpaper. The colours of flowers and tubes were semi-transparent pale blue and opaque white, respectively. In pre-test and test phases (see below), we offered nectar by inserting a cotton swab into a stem. One end of the swab was dipped into 20% sucrose solution (nectar) before insertion. Bee can drink the nectar from the cotton swab through the small tube at the base of a flower. In order to make a bee leave for another flower, we pulled out the swab about 4 seconds after the bee started probing. The time was too short for a bee to deplete nectar absorbed in the swab tip. We pushed the swab back after the bee landed on the next flower. Note that this method not only makes it easy to offer or withhold nectar, but also solves the difficulty of retaining nectar at the base of an inverted flower. The use of pipette tips as flower cups can be seen, for example, in Ishii (2005) and Makino & Sakai (2007), and 20% sucrose solution was used, for example, in Cnaani et al. (2006) and Worden et al. (2005).

Training phase

To train bees to forage in the cage, we placed six training "plants" (Fig. 1b) randomly on the table and let bees learn to collect nectar from them. Each training plant had a stem and two flowers that were the same as those used in the following test, except that the flowers were oriented horizontally, and nectar was provided continuously by a fixed cotton wick rather than a removable swab. The cotton conveyed nectar upward from a vial, allowing a bee to drink nectar *ad lib*. The gate of the nest was left open to allow bees to forage freely for a few days before testing. Note that bees in this phase did not have any experience with other flower orientations (i.e., upward- and downward-facing flowers), so they were experienced with regard to handling these flowers but naïve with respect to vertical orientation. To identify individual bees, we put correction fluid or numbered tags on the thoraxes of bees that learned flowers. We used those marked bees in the following test.

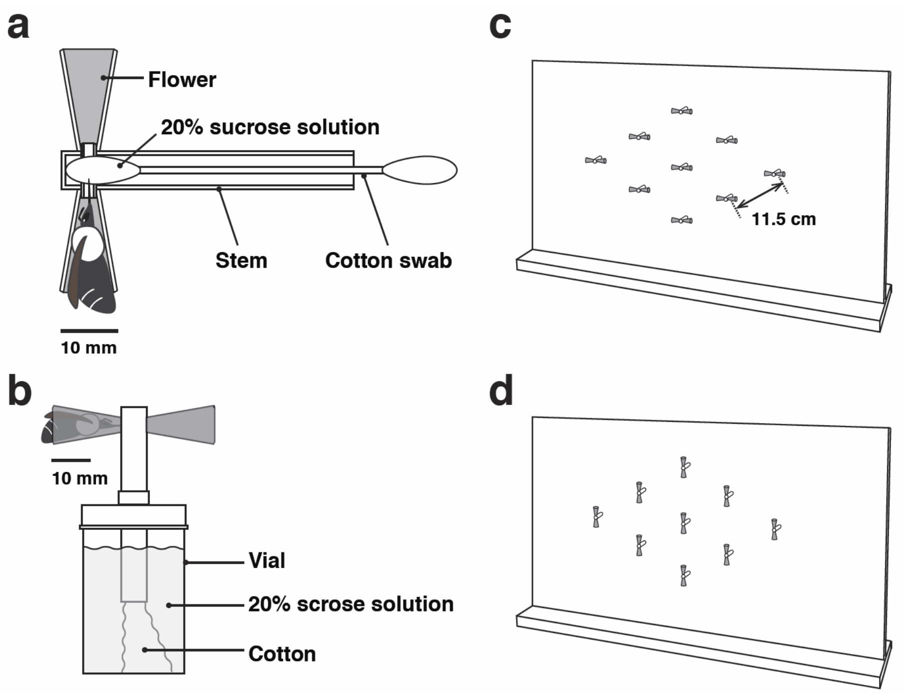

FIG. 1. Schematic views of artificial flowers and experimental arrays. (a) A cross section of upward- and downward-facing flowers on a stem pipe with a cotton swab inside. A bee can drink nectar from the swab until an observer pulls the swab. (b) A training plant with a pair of horizontal flowers. The cotton inside the stem conveyed nectar upward from a vial, allowing a bee to drink nectar unlimitedly. (c) The pre-test array with nine pairs of horizontal flowers. (d) The test array with nine pairs of upward- and downward-facing flowers.

Pre-test phase

Just before the test, we let a focal bee forage in a pre-test array (Fig. 1c) to accustom the bee to swab flowers arranged on a vertical board. The pre-test array comprised nine pairs of horizontal flowers arranged at 11.5 cm intervals in a triangular grid. Flowers were spaced 2.0 cm out from the board, and ranged between 105 cm and 128 cm above the floor. After the bee completed a foraging trip, we rotated each stem 90 degrees to change the pre-test array into the test array of paired upward- and downward-facing flowers (Fig. 1d). We arranged the pairs of flowers at five different heights to eliminate a possible tendency of bees to choose flowers at the same height (when pairs of flowers are placed at the same height, bees could appear to choose only upward- or downward-facing flowers simply by staying at the same height).

Test phase

Each bee was allowed to make three foraging trips in the test array. An observer noted the sequence of the orientations of flowers visited. We re-dipped swabs into nectar between foraging trips in most cases (there were only a few cases in which we did not, but re-dipped the swab of a flower while a bee was foraging another flower). Twenty-four bees were tested (12 bees from each colony). A bee made about 32 flower visits during a single foraging trip on average. We measured the length of the radial cell on the right forewing of each bee as an estimate of body size.

Analysis

To examine experience-dependent changes in the preference for upward-facing flowers, we applied a generalized linear model (GLM) with a logit link function and a binomial error distribution to the ratio of visits to upward-facing flowers to total visits. Foraging trips and individual bees were treated as fixed factors. We applied the same model to every pair of foraging trips for post-hoc comparisons (1st vs. 2nd, 1st vs. 3rd, and 2nd vs. 3rd). Alpha levels were adjusted by the sequential Bonferroni procedure with statistical significance determined at $P = 0.05$.

There were five levels of stem height, and to test whether there was any preference for certain height at the very first visit, we counted the number of visits for each level and performed a chi-square test with expected probabilities of 1/9, 2/9, 3/9, 2/9 and 1/9, from the lowest to the uppermost level, respectively. The P value was computed by Monte Carlo simulation with 10,000 replicates. All the analyses were performed using R version 2.13.0 (http://www.r-project.org/).

RESULTS

At the very first visit, 22 of 24 bees chose an upward flower (Fig. 2), a clear deviation from random choice (n = 24 bees, $P < 0.0001$, binomial test). There was also a significant tendency to choose the lowest stem at the first visit: the numbers of visits for each of the five levels were 9, 6, 8, 0 and 1, from the lowest to the uppermost level, respectively ($\chi^2 = 21.5$, $P = 0.001$). As shown in Fig. 3, the bees preferred upward- to downward-facing flowers over all three foraging trips (86.7% visits were to upward-facing flowers in total). This preference increased significantly from the first to the second foraging trip (Fig. 3). We also found that the preference significantly differed among bees (Tab. 1): the percentage of visits to upward flowers ranged between 61.5% and 100%, 65.2% and 100%, and 50.0% and 100%

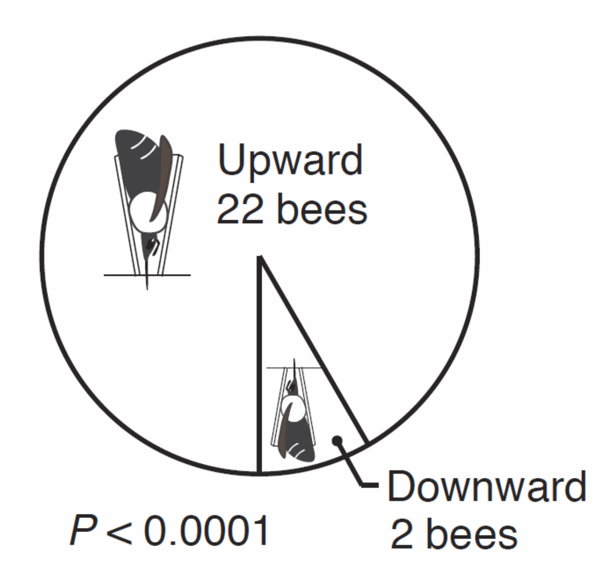

FIG. 2. The number of bees that chose upward- or downward-facing flowers at the very first visit (n = 24 bees).

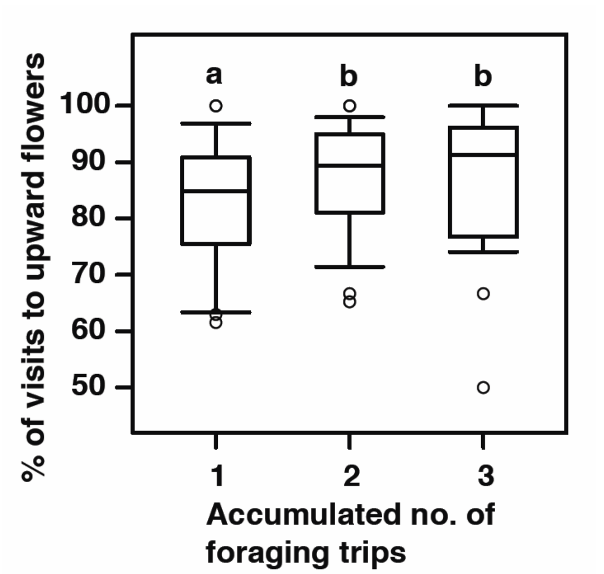

FIG. 3. Box-and-whisker plot of the percentage of visits to upward-facing flowers. The band in a box, the bottom and the top of the box, and the ends of the whiskers represents median, the 25th, 75th, 10th and 90th percentile, respectively (n = 24 bees). Small circles are outliers. Different letters indicate significant difference between foraging trips at sequential Bonferroni-adjusted alpha levels with statistical significance determined at $P = 0.05$.

TABLE 1. Analysis of deviance table on the proportion of visits to upward flowers

	df	Deviance	P
Foraging trip	2	9.7	0.0080
Individual bee	23	177.6	< 0.0001
Residual	24	74.6	

for the first, second and third trips, respectively. However, the variation was not significantly explained by colony (t = 1.96, df = 20.3, P = 0.064, Welch's t-test), nor body size (n = 24, Kendall's τ = –0.037, P = 0.801).

DISCUSSION

Without any prior experience with upward- and downward-facing flowers, *Bombus impatiens* workers overwhelmingly chose an upward-facing flower at the very first visit (Fig. 2), suggesting that bumble bees are predisposed to prefer upward-facing flowers. This innate preference grew stronger with experience, as evidenced by the significant increase in the proportion of visits to upward-facing flowers (Fig. 3). To our knowledge, this is the first demonstration of innate and learned preference of pollinators for upward-facing flowers. Although *B. impatiens* can certainly learn to handle pendent flowers (e.g., *Vaccinium angustifolium*, Stubbs & Drummond 2001), and may concentrate on them in the field, such learned preferences are evidently imposed on a template of upward-facing preference.

Costs and benefits of pendent flowers in terms of pollinator attraction

The strong preference indicates the possibility that bee-pollinated species with pendent flowers are more prone to pollen limitation (insufficient pollen deposition on a stigma) than those with upward-facing flowers due to their reduced attractiveness. It could be also possible that they invest more in floral traits for pollinator attraction such as petals or nectar to compensate this disadvantage. Future comparisons of those traits among congeneric flowering species with different flower orientations (e.g., *Campanula* and *Rubus*) may reveal some patterns associated with flower orientation.

In contrast, pendent flowers may ensure visits by faithful pollinators by preventing overexploitation of floral resources. All else being equal, reduced attractiveness should increase nectar standing crops of plants, which may let floral visitors specialize on the species (Heinrich 1976, 1979), and also encourage return visits by individual pollinators that learn the locations of beneficial plants (e.g., bumble bees: Burns & Thomson 2006; Makino & Sakai 2007; hummingbirds: Henderson et al. 2006). The reduced competition may further benefit plants by increasing their chance of being recruited into a pollinator's regular foraging route ("trapline"), which is predicted to increase mating distance and diversity, and also reduce inbreeding of plants (Ohashi & Thomson 2009).

Cause of preference for upward-facing flowers

The exact cause of the preference for upward-facing flowers remains unclear, but it is very likely that bees' tendency to remain upright when flying may predispose them to choose upward-facing flowers. Thus, the preference for upward-facing flowers may simply be a manifestation of general orientation preferences that arise from the basic body plan. The well-known preference for lower positioned flowers at the first visit and working upwards on vertical inflorescences (Waddington & Heinrich 1979; Harder et al. 2004) or experimental arrays (Makino 2008 and this study) may be the same sort of phenomenon, but it is quite possible for a bee to work upward while visiting downward-facing flowers, e.g., on *Digitalis* (Best and Bierzychudek 1982). We should be careful about the possible effect of the prior experience with horizontal flowers in the training phase, but it is hard to think that the experience gave any bias to upward-facing flowers.

The increased preference from the first to the second trips (Fig. 3) suggests that bees learned that upward-facing flowers were easier to handle. Although we did not measure handling time in this study, it is very likely that bees achieved shorter handling times on upward-facing flowers. Indeed, Laverty (1994) showed that naïve *B. rufocinctus* took longer to handle a pendent flower of *Apocynum androsaemifolium* than an upward-facing flower of *A. sibiricum*. In our experiment, we sometimes observed a bee landing on the outer surface of a downward-facing flower keeping its head up and then turning the head down to enter the corolla. We also occasionally saw a bee having difficulty in gripping on the slanting inner surface of a pendent flower, which supports the importance of landing platforms like lower lips of *Digitalis* (Percival & Morgan 1964), or surface structures to provide a better grip (Whitney et al. 2009). It seems worthwhile to see if such facilitations also encourage visits by bees and even invert the innate preference for upward-facing flowers. It would also be interesting to offer more concentrated nectars in downward-facing flowers to see if preferences can be switched.

Interspecific variations

Although *B. impatiens* showed strong preference, we should note that there may be variation among pollinator species, even within *Bombus*. Percival et al. (1968) found that while *B. terrestris* had no difficulty in exploiting pendent flowers of *Digitalis* foxgloves, some other species experienced physical difficulties in entering them. Such difference in handling techniques might lead to interspecific variation in the preference for flower orientation. Like *B. consobrinus*, which easily handle complex flowers of *Aconitum* from their first trials (Laverty 1988), there might be some specialist species for pendent flowers. Clearly, we need more experiments across many pollinator taxa including bees, flies, butterflies, birds, bats, etc., although obtaining naïve subjects will be much harder for vertebrates than for commercially available insects.

Conclusion

We demonstrated that bumble bees, which are known as frequent visitors to pendent flowers, do not necessarily prefer them; *Bombus impatiens* prefers upward-facing flowers if available. This finding indicates the overlooked cost of bearing downward-facing flowers for melittophilous species in terms of pollinator attraction. However, for plants in the presence of better pollinators, hanging flowers might be a good strategy to exclude inferior pollinators (Thomson 2003), as red floral colour reduces bee visitation to bird-pollinated flowers (Schemske and Bradshaw 1999). Pendent flowers are also expected to benefit plant fitness by increasing the precision of pollen transfer (Fenster et al. 2009), by enhancing pollen receipt and removal through increased handling time (Tadey & Aizen 2001), and by protecting nectar and pollen from rain (but see Tadey & Aizen 2001). Examining the balance of those costs and benefits will lead us a better understanding of selective pressures behind the evolution of pendent flowers. We hope our finding stimulates further investigations on other pollinator species. Even hummingbirds, which are usually assumed to have no preference, could have an innate preference for a specific orientation and thereby exert some pressure on floral traits.

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