Floral Constancy in Bumble Bees: Handling Efficiency or Perceptual Conditioning?
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Abstract Individual bees often prefer flowers of the same species that they are already foraging on, and other individual bees prefer other flowers. This "floral constancy" has classically been explained as a learned behavior by which bees avoid wasting time switching between handling techniques. Choice trails were given to *Bombus vagans* workers that were freely foraging in mixed and pure fields of *Trifolium pratense*, *T. repens*, *Viccia cracca*, and *Prunella vulgaris*. Contrary to expectation, (1) bees showed if anything a stronger preference for their flower type in pure fields where they lacked experience than in a mixed field where they had had the opportunity to learn, (2) there was greater constancy in a mixed field of the two morphologically similar *Trifolium* species than in a mixed field of the morphologically disparate *T. pratense* and *P. vulgaris*, and (3) bees were more willing to switch between flowers of distinct morphologies when the colors were similar than between flowers of distinct colors when the morphologies were similar. We suggest that constancy is due to some form of perceptual conditioning whereby individual bees become temporarily sensitized to one or a few floral cues.

Key words *Bombus vagans* · Conditioning · Constancy · Handling · Pollination

Introduction

Floral constancy is the tendency for individual animals foraging on flowers to specialize on one species or another, even when there is a mixture of flowers available. Darwin (1876) first proposed that constancy is the outcome of natural selection favoring bees with improved foraging efficiency. This explanation has taken on a classical aura in the literature (von Frisch 1953; Grant 1950; Bateman 1951; Manning 1956; Free 1963; Heinrich 1976; Waser 1986). Bees are seen as sequentially visiting similar flower types (and are thus constant) in order to minimize the time wasted on switching between handling techniques (von Frisch 1953). Different individuals are constant on different plant species, and thus all the floral resources are used by some bees but not by the same individuals (Heinrich 1976). Young inexperienced bees show less constancy than seasoned foragers (Laverty 1980), and it is believed that bees learn to be constant after initially working a variety of flower types (Heinrich 1979). The reason why constancy leads to efficiency is thought to be that animals have a limited memory capacity and can only remember how to quickly manipulate one or a few similar flower types at any given time (Lewis 1986; Waser 1986). Thus, by this classical view, constancy is seen as being due to a combination of neural limitations and the optimization of foraging return. An alternative view, which we will be led to, is that bees are constant due to a kind of perceptual conditioning by itself even without any optimization of efficiency. This view is consistent with recent findings by Laverty (1994) and L. Chittka, A. Gumbert and J. Kunze (unpublished work) that when bees do switch between flowers, the bees use very little additional time handling the flowers over that used when they are constant but they do use additional time in choosing between the flowers.

From the plant's point of view, constancy is beneficial because it promotes conspecific pollination. Less pollen is misplaced by the bee onto heterospecific flowers, a higher percentage of pollen is successfully transferred from and to flowers of the same species, and a higher rate of successful fertilization results. There have been two schools of thought regarding the

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origin of floral isolating mechanisms. Darwin (1859) treated floral isolating mechanisms as arising merely as incidental by-products of divergent evolution. Grant (1949) and others have imagined that plant species are sometimes selected specifically to have dissimilar flowers in order to promote pollinator constancy. Ethological isolating mechanisms, such as color differences, might have arisen through selection to avoid hybridization or the wastage of pollen in incompatible pollinations (Levin 1970; Straw 1972). Grant (1994) now finds that the evidence for such reinforcement is sparse, but it remains an interesting possibility that could explain the original finding of Grant (1949) that, in plants pollinated by animals capable of constancy, a high proportion of taxonomically useful characters are attributes of the flowers (Wilson and Thomson 1995). Following Bateman (1951) and Waser (1986), we suggest that a precondition for such adaptive reinforcement is that, as flowers become more distinct, bees become more constant. In other words, there would be no reinforcement if more and more divergent flowers did not result in stronger and stronger floral constancy by small evolutionary steps. Such an assumption is reasonable by the classical view of constancy, since, as flowers become more dissimilar, bees would presumably require additional time in learning and relearning different handling techniques.

Three methodologies exist for measuring patterns of floral constancy. Artificial flower experiments can be done in which one adjusts at will morphology, color, reward, and scent (von Frisch 1967). This could allow one to dissect the stimuli that lead to constancy, which would be most interesting. It would, however, be very difficult to make an entire field of artificial flowers in such a way as to manipulate the whole experiential foraging world of a set of bees, and thus far artificial flowers have always been crude substitutes for the ornately wrought natural objects that bees so subtly handle. Alternatively, array experiments, such as those of Waser (1986), can make use of real flowers in a natural setting. So far, however, the arrays have been too small to allow for control of the bees' whole world, and it is not clear how to best arrange the plants in space so that they give the bees an equal choice of the different flower types and an unbiased structure of rewards throughout the experiment. Finally, there is the bee interview technique of Thomson (1981) in which choices are provided on the end of a stick to naturally foraging bees in order to see which flowers they prefer. This approach has the disadvantage of not permitting tight experimental control of surrounding conditions or the dissection of different stimuli. It does, however, allow one to look at how bees vary in their choice patterns under different field conditions, for instance, in mixed fields where the bees have had ample opportunity to become familiar with the flower options being presented, and in pure fields where the options do not naturally occur and the bees are presumably unfamiliar with them. We interviewed bees, and our results call into question the classical view that bees are constant as a result of learning that it is inefficient to separately handle progressively distinctive floral morphologies.

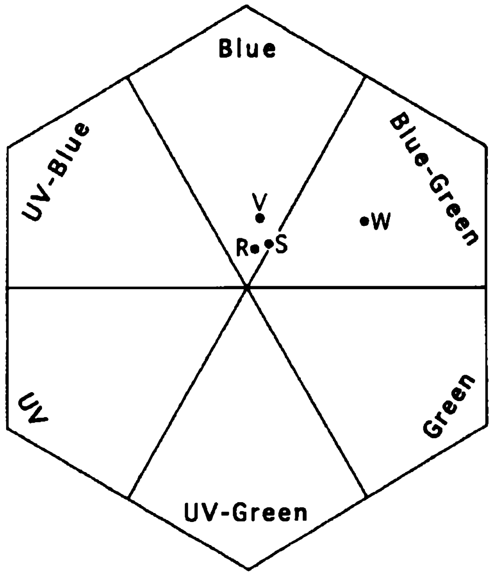
Materials and methods

Materials

We studied floral constancy of *Bombus vagans* Smith workers in open fields in central Massachusetts during the summer of 1994. *B. vagans* have long tongues and small bodies relative to other bumble bees in the area, and *B. vagans* was the most common species visiting the plants we studied. Those plants were red clover (*Trifolium pratense* L.), white clover (*T. repens* L.), cow vetch (*Vicia cracca* L.), and selfheal (*Prunella vulgaris* L.). A similar study was done by Laverty (1994), and some of his data are reanalyzed in the Appendix, showing that bumble bees are constant on these flowers. We observed *B. vagans* foraging for both nectar and pollen from all four species. In order to gather nectar, the bees inserted their tongues into the corolla tubes. In order to gather pollen, the bees generally "buzzed" the flowers and then packed pollen from their bodies into their pollen baskets while flying between inflorescences. Buzzing was less common when the bees were visiting selfheal than the other species.

The four plant species that we used varied in flower color and morphology. White clover is white with some individuals tinged pink. Red clover is pink. Vetch is violet. Selfheal is part violet and part white. Figure 1 shows the position of these four species on a hymenopteran spectral reflectance hexagon. White clover is "blue-green" to a bee; the other three are "blue" tending toward "mixed-colored" (Chittka et al. 1994). In terms of inflorescence structure, white and red clovers have similar head-like inflorescences, while vetch flowers are arranged in elongate racemes, and selfheal flowers are in short spikes. The clovers and vetch are fabaceous, with a lower keel petal, two lateral wing petals, and an upper banner petal that collectively form a closed floral tube. The vetch has a broader banner claw that overlaps the wings more completely than in the clovers. The ten stamens and the gynoecium of both the clovers

Fig. 1 Hymenopteran color hexagon and the colors of four flowers that were studied (*W* white clover, *R* red clover, *V* vetch, *S* selfheal). See Chittka (1992) for details on the axes of the hexagon



and the vetch are held between the keel and the wing petals, with the tips of the filaments and the stigma curving upward. Selfheal is a mint whose bilabiate flowers form an open tube. The upper corolla lip of the flower is galeate-hooded, and the four stamens and gynoecium are situated beneath the roof of the galea with the anthers and stigma facing down.

Bees handle red and white clover very similarly. Upon landing on a clover, a bee spreads apart the wing petals with her legs, and presses her head down along the inside roof of the elongated concave banner petal. Red clover has a longer floral tube, and bees have to probe more deeply than they do when visiting white clover. In the process of probing, the keel petal is pushed downward and the anthers and stigma are exposed. The bee then buzzes the flower, shaking pollen onto the ventral parts of her body.

Vetch flowers are morphologically distinct from both the clovers and require a slightly different handling technique. The banner petal is much broader, and does not fit as snugly against the bee's head as does the banner petal of either clover species. Furthermore, a vetch banner petal cannot simply be pushed up by the bee inserting her head and tongue along the roof of the flower. Rather, bees insert their forelegs under the claw and push down on the wings and keel while also spreading the wing petals apart with their midlegs. In addition to these subtle differences of manipulation within a flower, bees on vetch are dealing with a vertical inflorescence that they forage upward on, whereas bees on clovers move laterally around a head of flowers.

The flower shape of selfheal is extremely different from any of the fabaceous species, and is handled differently by bees. The lower lip of a selfheal flower is broad and provides a landing platform for the bee, which she embraces with her forelegs upon landing on the flower. She then inserts her head and extended tongue directly into the open mouth, probing deeply until her head presses snugly against the galeate-hooded upper lip. This brings her head directly against the anthers and stigma, thus promoting pollen transfer nototribically. Since the bees rarely buzz selfheal flowers, their manipulation of pollen seems less intentional than with the clovers or vetch.

Methods

We measured floral preferences of freely foraging bees by interviewing them with an interview stick (Thomson 1981, Thomson et al. 1983). The interview stick was 80 cm long with a short piece of thick plastic tubing attached at one end, perpendicular to the stick, and in the shape of a V. Two picked inflorescences could then be inserted into the two arms of the V, where they were held about 9 cm apart. Holding the other end of the stick, one of us could then interview a bee that was on an unpicked inflorescence by holding the stick such that the two picked inflorescences were equally close to her. When bumble bees are busy probing flowers, they do not seem to be disturbed by the presence of the interview stick or the interviewer. When they are flying between inflorescences, they are more easily perturbed. We only approached bees to be interviewed when they were already on an unpicked inflorescence. Since bees tend to move on to nearby inflorescences, they would often choose one of the two choices we were offering. When a bee flew to one of our choices and probed the flowers in that inflorescence, we recorded what species the bee came from, which option it went to, and what the other option was.

The flowers we used were picked fresh for each interview from the field where we were doing our interviews, or, when a species to be used in an interview was not present in the focal field, we would pick flowers elsewhere and keep them fresh for up to 1 h in plastic bags in a styrofoam box. We picked flowers without regard to how much nectar they might have in them or how recently they might have been visited. Our intent was to match the conditions that the bees were naturally encountering. Newly picked inflorescences were used after each interview. About fifty interviews were conducted for each pair of options. For instance, in a mixed field of red and white clover, 51 interviews were done of bees coming off red with a choice of red or white, and 50 interviews were done of bees coming off white with a choice of white or red. Since bees were not identified as individuals, the same bee may have been interviewed repeatedly; however, we tried to avoid reinterviewing the same bee immediately after an interview.

We interviewed *B. vagans* workers in a variety of fields, both where two species were completely intermixed and where there was essentially a monoculture: in a mixed red and white clover field, in a mostly white clover field with a few red clover, in a pure vetch field, and in a red clover field with selfheal but without white clover or vetch. The fields were all within 2 km of each other, and they were separated from each other and other flowering fields by at least 100 m, wooded areas, and roads. Bees in all fields were interviewed for similar numbers of days (3–5) and across similar times of day (midmorning to midafternoon). In the mixed fields, particularly the red and white clover field, bees were continuously encountering two or more species, and by the classical view one would expect heightened constancy to one floral type. In the pure fields, bees had very little recent experience with other plant species, and one would expect that the bees had no opportunity to learn to be constant. The bees probably had encountered all species at some time during their life, and bees are known to be able to remember flowers for months, at least in a vague way. The classical explanation of constancy, however, rests on an assumption that the memory or the motor training of exactly how to handle flowers is a short-term phenomenon, and it seems safe to assume that the bees in the mixed fields had much more recent experience than the bees in the pure fields. In addition to interviewing, we also followed naturally foraging bees in our mixed fields and recorded the sequence of species that they visited (Heinrich 1976).

Results

Generally bees did not choose equally between the two flower species offered, as demonstrated by the goodness-of-fit tests in Tables 1–3. When given the choice of the flower they were already on or a different one, in most cases they choose to be constant. There were a few telling exceptions to be noted below as each field is treated in turn.

Table 1 *Bombus vagans* choices in a mixed red and white clover field (*W* white clover, *R* red clover)

Goodness of fit H_0: 1 : 1

n	Percent of times chosen[a]	G
50	68% W ← W → R 32%	6.63^{*}
51	88% R ← R → W 12%	33.76^{***}

Test of independence

	To W	To R
From W	34	16
From R	6	45

$G = 33.76^{***}$; $r_n = 0.56$

$^{*}P < 0.05$, $^{***}P < 0.001$

[a] The center letter represents the flower that the bees came from; the flanking letters and percentages are the flower that the bees went to

In the completely mixed red and white clover field, bees were significantly constant (Table 1): those on white clover tended to choose white clover; those on red tended to choose red; and the test of association was significant with an association index of $r_n = 0.56$ (Zar 1984, p. 323). This was a field with nearly equal representation of both clovers. When bees encountered (and had presumably experienced) both clover species, they specialized to some degree on one species or the other. The results from the visit sequences of freely foraging bees showed that bees only occasionally switched between flower species in mixed field conditions (Fig. 2). Some bees preferred white clover, e.g., bee 5, while others preferred red clover, e.g., bee 6. Specialization did occur, although bees were not nearly 100% constant. For instance, bee 2 was particularly prone to switching.

In the predominantly white clover field, which had a few contaminant red clovers, bees still significantly preferred white clover when the other option was red clover (Table 2, top panel). Oddly enough, they were not significantly constant when the other option was vetch. When offered vetch or red clover, bees did not significantly prefer one option over the other, and a heterogeneity in goodness-of-fit tests comparing red versus white to vetch versus white confirms that there is not much preference for one or the other ($G_{\text{heterogeneity}} = 1.87$; $P > 0.1$; Sokal and Rohlf 1981, p. 722) . The important result is that bees chose red clover as regularly in this field (where they rarely encountered red clover) as they did in the red and white mixed field, i.e., 68% of the time.

In the pure vetch field, the bees were extremely reluctant to go to either the unfamiliar red clover or the unfamiliar white clover (Table 2, middle panel). In fact, we had a difficult time getting bees to choose between red and white clover. They shunned both, which is why our sample size is 12 in this case. In addition to these 12, we attempted to interview 41 bees that each refused us ten times. After ten rejections, we went on to interview a different bee. All three goodness-of-fit tests were extremely significant, reflecting how strong the preferences were in this field. A comparison of the options of vetch versus white clover against vetch versus red clover showed that bees had no significant preference for either clover when the other option was vetch ($G_{\text{heterogeneity}} = 0.35$; $P > 0.1$).

In the red clover field, which also contained some selfheal and a few very infrequently visited white clover flowers, bees strongly preferred red clover (Table 2,

Fig. 2 *Bombus vagans* foraging paths over 40 consecutive flower visits in a field of mixed red and white clover (*W* white clover, *R* red clover, underlining indicates runs of all white or all red)

Bee 1: R-R-R-R-R-R-R-R-W-R-R-R-R-R-R-R-W-R-R-R-R-R-R-R-R-R-R-
R-R-R-R-R-R-R-R-R-R-R-R-R

Bee 2: W-W-W-R-W-R-R-W-W-W-R-R-R-W-W-W-R-R-W-W-W-R-R W-R-
W-W-W-R-R-W-R-R-W-R-R-R-R-R-R

Bee 3: W-W-R-W-W-R-W-W-W-W-W-R-W-W-W-W-W-W-W-W-W-W-W-
W-W-W-W-W-W-W-W-W-W-R-W-W-W-W-W-

Bee 4: R-W-W-W-R-W-W-W-W-W-W-W-W-W-R-W-W-W-W-W-W-W-W-R-
W-W-W-R-W-W-W-W-W-W-W-W-W-W-W-W

Bee 5: W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-
W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W-W

Bee 6: R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-
R-R-R-R-R-R-R-R-R-R-R-R

Table 2 *B. vagans* choices in pure white clover, red clover, and vetch fields (*W* white clover, *R* red clover, *V* vetch)

	In a white clover field[a]	
n	Percent of times chosen[a]	G^b
53	68% W ← W → R 32%	6.97**
51	55% W ← W → V 45%	0.49^{ns}
50	60% R ← W → V 40%	2.01^{ns}
	In a vetch field	
50	98% V ← V → W 2%	59.51***
50	96% V ← V → R 4%	52.52***
12	92% R ← V → W 8%	9.75**
	In a red clover field	
51	98% R ← R → W 2%	60.86***
50	80% R ← R → V 20%	19.27***
50	94% V ← R → W 6%	46.62***

$^{ns}P > 0.1$, $^{**}P < 0.01$, $^{***}P < 0.001$

[a] The center letter represents the flower that the bees came from; the flanking letters and percentages are the flower that the bees went to

[b] G values for a goodness-of-fit H_0: 1:1

Table 3 *Bombus vagans* choices in a red clover and selfheal field (*R* red clover, *S* selfheal)

	Goodness of fit H_0: 1:1	
n	Percent of times chosen[a]	*G*
62	65% R ← R → S 35%	5.30*
50	72% S ← S → R 28%	10.02**

Test of independence

	To R	To S
From R	40	22
From S	14	36

$G = 15.18^{***}$; $r_n = 0.36$

$^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

[a] The center letter represents the flower that the bees came from; the flanking letters and percentages are the flower that the bees went to

Bee 1: S-S-S-S-S-S-R-S-S-R-R-R-R-R-R-R-R-R-R-R-R-R-S-S-R-S-R-S-S-
S-S-S-S-S-S-S-S-R-R-R-R-R-R-S-R-S-R-S

Bee 2: R-R-S-R-R-R-R-R-R-R-R-R-S-R-R-S-R-S-R-R-R-R-R-R-R-R-R-R-
R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-
R-R-R-R-R-R-R-R-R

Bee 3: R-S-R-S-R-R-S-S-R-R-R-S-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-
R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-
R-R-R-R-S-R-R-R-R-R-R-S-R-R-R-R-R-R-R-R-R-R

Bee 4: R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-
R-R-R-R-R-R-R-R-R-R-R-R-R-R

Bee 5: R-R-R-R-R-R-R-R-S-R-S-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-
R-S-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-S-R

Bee 6: R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-
R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-R-S-R-
R-R-R-R-R

Fig. 3 *B. vagans* foraging patterns over a minimum of 40 visits in a red clover field with selfheal (*R* red clover, *S* selfheal, underlining indicates runs of all red clover or all selfheal)

bottom panel). This was true whether the other option was white clover or vetch, although a test of heterogeneity revealed that bees were significantly more constant on red clover when white clover was the other option than when vetch was ($G_{\text{heterogeneity}} = 9.65$; $P < 0.01$). Also when directly choosing between white clover and vetch, the bees were more inclined to visit vetch than white clover when coming off red clover, even though white clover and red clover are handled nearly identically and are more similar overall than vetch and red clover. Of particular interest is the fact that bees were much more constant on red clover in this pure red clover field than in the red and white clover mixed field. Goodness-of-fit tests show that there was significant constancy on red clover in both fields; however, examining the heterogeneity between these fields revealed that bees went to red clover more often in the red clover field than in the mixed field ($G_{\text{heterogeneity}} = 4.23$; $P < 0.05$).

A week later in the same field, we turned our attention to comparing red clover to selfheal, which was then increasing in flower number. The bees were significantly constant (Table 3). Bees on red clover chose red clover more times than not. Bees on selfheal chose selfheal. The test of independence was significant, with an association index of $r_n = 0.36$. This was weaker than the $r_n = 0.56$ of the red and white clover mixed field. A test of heterogeneity between the two tests of association from the two fields showed that bees were significantly more constant between red clover and white clover than between red clover and selfheal ($G_{\text{heterogeneity}} = 5.95$; $P < 0.05$). This is despite the close morphological similarity in red and white clover as compared to the much greater disparity between red clover and selfheal. When we followed freely foraging bees in the red clover and selfheal mixed field, we found that they frequently switched between species while naturally foraging (Fig. 3). Overall, there appears to have been a general preference for red clover. It is important to note that red clover was much more abundant than selfheal in this field, and there may not have been enough selfheal for any bee to major on it (*sensu* Heinrich 1976).

These results are not yet replicated at the level of fields of different types. Also, we have not been able to measure constancy in fields of evenly mixed red clover and vetch, white clover and vetch, white clover and selfheal, or selfheal and vetch.

Discussion

We predicted that if bees are constant because they learn to minimize handling time, then they should be more constant in a mixed field where they have already encountered and evaluated the different species, and they should be less constant when presented with an unfamiliar species in a pure field. On the other hand, if bees are constant due to a purely ethological mechanism, such as formulating a search image, then they should if anything be more constant in the pure field than in the mixed field. We found the latter pattern. Bees were equally constant on white clover regardless of whether it was a mixed red and white clover field or an almost pure white clover field. Moreover, bees on red clover were actually more constant in an almost pure red clover field than in a mixed red and white clover field.

We further predicted that if bees are constant as a result of minimizing handling time, and thus maximizing foraging efficiency, then they should show less constancy in a field where the similar red and white clovers grow intermixed than in a field where the dissimilar red clover and selfheal grow mixed. However, once again our results went against this idea that constancy is a result of minimizing handling time. The higher constancy index that resulted for the red and white clover mixed field as compared to the red clover and selfheal mixed field shows that, in this case, bees were actually more constant between the morphologically similar clover flowers, and less constant between red clover and the mint selfheal. The bees more readily switched between two flowers that required different handling techniques.

Lastly, we predicted that if the classical view is correct, then bees provided with two unfamiliar flower options should choose the flower that is more similar in overall morphology and expected handling time to the one they are already familiar with. In the red clover field where bees rarely encountered white clover or vetch, bees should have chosen to go from red clover to white clover over going to the morphologically dissimilar vetch. Yet, once again our results went against this prediction. When bees in a red clover field were presented with vetch versus white clover, they usually choose vetch. Color is the one way in which red clover is more like vetch than white clover. A correspondance between degree of constancy and bee color has been found in several other systems as well, some of which were composites that are all handled similarly (Waser 1986; L. Chittka, A. Gumbert, and J. Kunze, unpublished work; Chittka unpublished work).

Our results, then, suggest that the classical view is somewhat incorrect. Bees are not constant primarily because they learn to minimize handling time on flowers, and they are not always more constant when the flowers are more disparate. We doubt that bees adopt constancy after evaluating their expected returns from constant behavior versus from inconstant behavior, and we doubt that each detail of floral morphology and handling technique is important in determining the degree of constancy. Instead, it seems plausible that bees are constant for an ethological reason that involves some form of perceptual conditioning. We imagine that as a bee becomes involved in the rhythm of her work, certain floral cues, such as color or scent, come to be temporarily fixed in her mind. Once she is sensitized to perceive one or a few key features of a search image, say a bee-blue color, then that bee-blue color triggers the proper conditioned response of visiting the next bee-blue flower that draws her attention (L. Chittka, A. Gumbert, and J. Kunze, unpublished work). By our alternative view, constancy is merely a byproduct of a neurobehavioral bias that is part of a general foraging system. Of course, that foraging system may have been shaped by natural selection so as to maximize efficiency, or at least to avoid wasting time on visits to objects that are unlike the ones that have recently proven to be rewarding. The foraging choices of bees are certainly based on both handling and perception. The two are not mutually exclusive, but our data suggest that bees have a preference for the flower type they are already on even when they have not had any recent opportunity to evaluate differences in handling.

The implications of the alternative view for the evolution of floral characters might be considerable. First, our results contrast with those of Bateman (1951) and Waser (1986). They found that bees were more constant when the plants were more taxonomically and morphologically distant than when the plants were closely similar. This now seems as if it might not be a particularly universal rule. Second, perceptual conditioning might mean that reinforcement can only take place on the few characters that animals key in on in forming their search image, but on these characters selection might be quite focused. It would be interesting to know exactly what characters can lead to increased floral constancy. Color, odor, size, and the brokenness of the floral outline seem like good candidates, whereas the grooving of nectar spurs, the placement of landing platforms, and the positioning of anthers seem like they might be selected on to encourage visitation but not particularly to encourage constancy. Third, by the classical view, if and when constancy characters are favored, it would seem to be most likely to happen through group selection after a local patch of flowers has become more distinctive by other evolutionary processes – a distinctive individual by itself would probably be selected against because it would not look like normal conspecifics. However, by the alternative view it is more reasonable to think that a peculiarity in an individual might not decrease bee movement between conspecific flowers while it still could decrease bee movement between heterospecific flowers. This is because when we think of a neurological trigger, the degree of difference in some floral character like color might not be additive in terms of bee recognition, i.e., psychological distances (A to B) + (B to C) $\neq$ (A to C).

Additional comparisons should be done to confirm the patterns we have found. We are particularly keen on measuring constancy in a mixed vetch and red clover field versus a pure vetch field and a pure red clover field. Although we replicated our trials within each field, we have no replication of different pure and mixed fields. Also, it would be valuable to repeat our study with another set of plants that vary in ways other than the ways in which our plants varied. For instance, would consistent results emerge from a set of plants that differed in scent but not in color, or that differed more radically in the ways bees handle them? Beyond gathering more data of the sort we have already collected, the alternative view we have proposed could be explored by other sorts of experiments and different types of data. If it succeeds in accounting for further oberservations, it will serve as one example of how behavioral ecology can be improved by postulating ethological phenomona.

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Appendix 1

The goodness of fit of Laverty's data to H_0: 1:3

Laverty (1994) also presented data in which bumble bees were interviewed with selfheal, vetch, red clover, and a white clover (though not the same species as we studied, rather *Trifolium hybridum*). He presented all four flowers at a time in a bouquet, and *Bombus fervidus* workers chose one of the four. Thus, the null expectation was that the bees would visit the species they were coming from one quarter of the time. He tested different hypotheses, and as a result his Table 1B at first glance contradicts the view that bees are biased in favor of the species they are coming from. We, therefore, retabulate his data in Table A1.

Table A1 *Bombus fervidus* choices from four flower species in a mixed field. Percentages should be compared to 25% and 75%

n	Percent of times chosen[a]	G[b]
135	33% S ← S → other 67%	3.91*
166	49% R ← R → other 51%	43.46***
155	39% V ← V → other 61%	15.42***
72	44% W ← W → other 56%	12.81***

*$P < 0.05$, ***$P < 0.001$

[a] The center letter represents the flower that the bees came from; the flanking letters and percentages are the flower that the bees went to

[b] G values for a goodness-of-fit H_0: 1:3

References

Bateman AJ (1951) The taxonomic discrimination of bees. Heredity 5: 271–278

Chittka L (1992) The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. J Comp Physiol 170: 533–543

Chittka L, Shmida A, Troje N, Menzel R (1994) Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. Vision Res 34: 1489–1508

Darwin C (1859) The origin of species. Murray, London

Darwin C (1876) The effects of cross and self fertilisation in the vegetable kingdom. Murray, London

Free JB (1963) The flower constancy of honeybees. J Anim Ecol 32: 395–402

Frisch K von (1953) The dancing bees. Harcourt Brace, New York

Frisch K von (1967) The dance language and orientation of bees. Harvard University Press, Cambridge

Grant V (1949) Pollination systems as isolating mechanisms in angiosperms. Evolution 3: 82–97

Grant V (1950) The flower constancy of bees. Bot Rev 16: 379–398

Grant V (1994) Modes and origins of mechanical and ethological isolation in angiosperms. Proc Natl Acad Sci USA 91: 3–10

Heinrich B (1976) The foraging specializations of individual bumblebees. Ecol Monogr 46: 105–128

Heinrich B (1979) "Majoring" and "minoring" by foraging bumblebees, *Bombus vagans*: an experimental analysis. Ecology 60: 245–255

Laverty TM (1980) The flower visiting behaviour of bumble bees: floral complexity and learning. Can J Zool 58: 1324–1335

Laverty TM (1994) Costs to foraging bumble bees of switching plant species. Can J Zool 72: 43–47

Levin DA (1970) Reinforcement of reproductive isolation: plants versus animals. Am Nat 104: 571–581

Lewis AC (1986) Memory constraints and flower choice in *Pieris rapae*. Science 232: 863–865

Manning A (1956) Some aspects of the foraging behavior of bumblebees. Behavior 9: 164–201

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. WH Freeman, New York

Straw R (1972) A Markov model for pollinator constancy and competition. Am Nat 106: 597–619

Thomson JD (1981) Field measures of flower constancy in bumblebees. Am Midl Nat 105: 377–380

Thomson JD, Maddison WP, Plowright RC (1982) Behavior of bumble bee pollinators of *Aralia hispida* Vent. (Araliaceae). Oecologia 54: 326–336

Waser NM (1986) Flower constancy: definition, cause, and measurement. Am Nat 127: 593–603

Wilson P, Thomson JD (1995) How do flowers diverge? In: Lloyd DG, Barrett SCH (eds) Floral biology. Chapman and Hall, New York

Zar JH (1984) Biostatistical analysis, 2nd edn. Prentice-Hall, Englewood Cliffs