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The effect of variation among floral traits on the flower constancy of pollinators

The interaction between floral traits and pollinator behavior has been an important force in the coevolution of plants and their animal pollinators. An element of conflict underlies this interaction because the ideal behavior of the pollinator from the plant's point of view may often diverge from that dictated by the pollinator's own self-interest. Because of their immobility, outcrossed plants require a reliable courier that has a high probability of placing their pollen where it has a chance of fertilizing a conspecific ovule. Pollen finding an inappropriate stigma is effectively wasted, and deposition of heterospecific pollen may block receptive sites on the stigma and reduce seed set (e.g., Waser 1978, 1983; Thomson *et al.* 1981; Campbell & Motten 1985). Thus, plants should benefit if pollinators tend to move sequentially among flowers of the same species, a pattern that an optimally foraging pollinator should rarely adopt unless energetic returns from one plant species regularly exceed those from a mixed diet of some or all of the flower species available. More often, pollinators distribute themselves in an ideal free pattern across resources (Dreisig 1995), thereby minimizing differences in rewards among many different plant species, a pattern that should make generalist foraging the best option.

Yet pollinators often sequentially visit the flowers of one species even though they are bypassing flowers of other available, rewarding plant species (e.g., Grant 1950; Manning 1957; Free 1970; Waser 1983, 1986; Lewis 1989; Goulson & Cory 1993; Laverty 1994*b*). This "flower constant" foraging behavior has been described in many taxa, primarily honeybees (e.g., Wells & Wells 1986; Hill *et al.* 1997), bumble bees (e.g., Free 1970; Heinrich *et al.* 1977), and butterflies (Lewis 1986), but also more recently in solitary bees (Gross 1992), beetles (De Los Mozas Pascual & Domingo 1991), and dipterans (Goulson & Wright 1998).

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Chittka *et al.* (1999) recently reviewed the many explanations that have been proposed to account for pollinator flower constancy and suggested that constancy probably has multiple causes. The most popular explanations for floral constancy invoke some sort of limitation on the cognitive abilities of pollinators to process, store, or recall information about multiple flower types at the same time (e.g., Waser 1983, 1986; Lewis 1993; Dukas 1998; Goulson 2000; but see Menzel, this volume). Two main hypotheses concerning the relation between flower constancy and the cognitive abilities of pollinators have been tested experimentally; these are considered below.

### **Darwin's hypothesis**

The first hypothesis arises from Darwin's (1876) widely quoted statement:

That insects should visit the flowers of the same species for as long as they can is of great significance to the plant, as it favours cross-fertilization of distinct individuals of the same species; but no one will suppose that insects act in this manner for the good of the plant. The cause probably lies in the insects being thus enabled to work quicker; they have just learnt how to stand in the best position, and how far and in what direction to insert their proboscides.

Darwin's explanation implies that pollinators learn and remember the motor pattern or handling skill associated with flowers of a particular species. Bumble bees (Heinrich 1976, 1979; Laverty 1980, 1994a; Laverty & Plowright 1988) and butterflies (Lewis & Lipani 1990) are capable of learning and remembering a variety of different flower-handling skills. Motor patterns needed for working simple flowers with exposed nectar are learned quickly, while more complex flowers with concealed nectar are more difficult to learn. Waser (1983, 1986) interpreted Darwin's statement as meaning that pollinators are constant because they are limited in the number of handling skills that they can remember simultaneously. Lewis (1986) added the idea that learning additional flower-handling skills may interfere with a pollinator's ability to recall a previously learned handling skill. This combined hypothesis, which has been referred to as "Darwin's interference hypothesis" (Woodward & Laverty 1992), suggests that pollinators are constant to the flowers of one or a few plant species to minimize the costs of relearning flower-handling skills after every switch.

Attempts to test Darwin's hypothesis have looked for evidence of increased flower-handling times immediately following a switch between flower types requiring different handling skills in butterflies (Lewis 1986; Goulson *et al.* 1997) and bumble bees (Woodward & Lavery 1992; Lavery 1994b; Gegeer & Lavery 1995, 1998). The most common design has been to train a test group of individual pollinators to work flowers of species A, then to switch them to learn a second flower type (B), before finally retesting them again on flower type A. If handling times during the retesting period are significantly greater than those recorded during initial training on flower type A, then the increase is attributed to some sort of negative effect from learning a new type, or simply forgetting the motor patterns associated with flower type A with the passage of time. To separate these two possible sources of reduced performance, a control group is run to assess the contribution of forgetting with the passage of time. The difference in retest handling times between the test and control groups is attributed to the effect of switching between flower types requiring different handling skills.

Does switching flowers increase handling times? The answer depends on several factors, including the difficulty and number of new flower-handling skills learned. Data from many studies that measured the increase in flower-handling time attributed to switching (shown as a percentage above the flower handling time for an experienced pollinator) are summarized in Fig. 1.1. Switching between two different handling skills generally involves an increase in the handling time for experienced foragers of only 0–2 s – or a 0%–100% increase in handling time – although one study of butterflies (Lewis 1986) found a 300% increase. In general, these elevated times are still 10–50 times lower than the handling time of naïve individuals learning the skill for the first time. Switching among three or more different flower-handling skills results in much longer handling times, approaching those for naïve individuals, especially if the additional flower types are difficult. These results suggest that switching may weaken or in some cases even erase from memory the motor patterns that bees have learned for handling flowers (see Chittka *et al.* 1999 for discussion).

One complication in interpreting many of these studies is that the animals tested made the switch among different flower handling methods only once. Dukas (1995) found that bumble bees switching among different foraging tasks for the first time showed a 22% reduction in choosing the correct flower color, but this reduction disappeared with practice. Moon (1999) recently demonstrated that bumble bees could

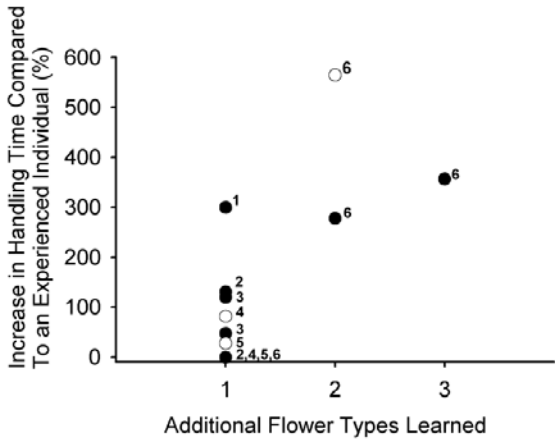


Fig. 1.1 Increase in handling times for flower type A following switches to additional flower types. Increase expressed relative to the mean handling time for experienced foragers. Circles denote the floral complexity of the additional flower type(s) learned (closed = simple; open = complex). Data taken from: (1) Lewis (1986); (2) Goulson *et al.* (1997); (3) Woodward & Lavery (1992); (4) Lavery (1994*b*); (5) Gegear & Lavery (1995); (6) Gegear & Lavery (1998).

learn to switch between two different flower-handling skills without penalty. For bees working three flower types, however, a residual cost of 1.1 s (a 52% increase in handling time) remained, despite repeated practice. These costs may seem small, but could add up over many foraging episodes in the life of an individual.

Are switching costs related to constancy? The key point here is to find a relationship between the magnitude of switching costs and the tendency to move sequentially among like flower types. The larger the penalty for switching, the more the forager would benefit from being constant, all else being equal. Although Lewis (1986) found strong constancy to a single plant species and long relearning times when butterflies switched species, studies with bumble bees have found no consistent link between the magnitude of switching costs and flower constancy (Woodward & Lavery 1992; Lavery 1994*b*; Gegear & Lavery 1998; Moon 1999).

### Search image hypothesis

The second hypothesis is based on the “search image” concept outlined by Tinbergen (1960). Tinbergen argued that in order to increase the efficiency of detecting one prey type, a predator performs “a highly selective sieving operation on the visual stimuli reaching the retina,” forming a

“searching image” for that prey type. It appears that the perceptual mechanism behind search image effects is related to the “run effect”: animals tend to improve their performances by selecting “runs” of one prey type, even though other types are available (Bond & Riley 1991). For example, Pietrewicz & Kamil (1979) found that blue jays (*Cyanocitta cristata*) could find one species of cryptic moth better after practice runs of that species alone, but did not improve if runs involved alternation of two different moth species.

Although many authors have suggested that search images can account for flower constancy (e.g., Levin 1978; Waser 1986; Dukas & Real 1993; Wilson & Stine 1996; Goulson 2000), there is little empirical evidence for the formation of search images in pollinators. In field experiments with flower species that differed in both handling skill and color, Wilson & Stine (1996) found that individual bumble bees visited flowers of similar color but different handling skills (e.g., pink/purple-flowered red clover and self-heal), but not flowers differing in color but with the same handling method (e.g., purple-flowered vetch and white clover). They argued that bees were constant because they formed a search image based on flower color. Thus, as bees sequentially visited the flowers of one species, they became conditioned to the color of that flower, and subsequently tended to visit similarly-colored flowers, even of another plant species.

Most discussions of search image assume that the predator is searching for cryptic prey types (e.g., Dawkins 1971*a, b*; Bond & Riley 1991; Reid & Shettleworth 1992); however, Tinbergen did not explicitly state this condition as a component of the hypothesis. Can flowers be cryptic? Goulson (2000) recently proposed that flowers are effectively cryptic when viewed against a background of plant species with similarly colored flowers. In a field experiment, Goulson found that bumble bees took twice as long to find flowers of one yellow-flowered species in an area containing several other yellow-flowered species, compared with their rates in an area where the background flowers were not yellow. However, in this study only flight times to the next nearest flower were assessed, and no data were presented on the relationship between constancy and the floral background mix encountered by pollinators.

### **Flower-handling skills or search image for floral features?**

Many authors have suggested that hypotheses for flower constancy based on flower handling and those based on search image are not mutually

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exclusive (Waser 1986; Dukas & Real 1993; Wilson & Stine 1996; Dukas 1998; Goulson 2000). In fact, under natural foraging conditions it is difficult, if not impossible, to separate the two. Every flower has a particular motor pattern associated with a set of sensory cues, such as color, odor, size, and shape. Thus, it is probable that studies using real flowers to test Darwin's hypothesis (supposedly manipulating only flower-handling skill) or the search image hypothesis (supposedly assessing a single floral signal such as color) have been confounded by between-species differences in a variety of other floral traits besides the one of interest. For example, the increased flower-handling times following switches between two flower species observed by Lavery (1994*b*) and Lewis (1986) may have been affected by other uncontrolled floral differences besides handling method such as color and scent.

Similarly, in field experiments testing the search image hypothesis (such as Wilson & Stine 1996), it was concluded that visitors became conditioned to legume flowers of the same color (e.g., vetch and red clover) and ignored differently-colored flowers (white clover) that apparently had the same flower-handling method. However, in this example, corolla tube length may also have been a confounding factor (Lavery 1994*b*): white clover has a short tube relative to the other two legumes, and bees may display some degree of constancy to tube length. These points underscore the advantages of testing hypotheses about effects of floral traits on pollinator behavior under carefully controlled conditions where traits can reasonably be manipulated one at a time.

### **Trait variability hypothesis**

Given that both motor pattern and sensory stimuli are closely linked together (e.g. Chittka & Thomson 1997), perhaps it is time to take a more comprehensive approach to investigating the effect of floral traits on pollinator behavior. Instead of investigating pollinator choice patterns as a separate response to either handling skill or single traits such as flower color, selective foraging patterns such as flower constancy and learned preferences (an overall bias in choice towards some of available flower types) may be responses to variability over a wide range of floral traits. A key idea in this "trait variability hypothesis", as we have called it, is that pollinators are faced with two fundamentally different types of variation among flower types. First, there can be variation within a single trait (herein referred to as states of a trait). For example, three flower color

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morphs (blue, purple, or pink) would represent three states (blue, purple, and pink) of the trait (color). Second, flower types may also be defined by variation among several floral traits. For example, flowers from two plant species might show variation in both color (yellow and blue) and size (large and small).

Although the effect of variation within and among floral traits on pollinator behavior has not been previously compared in manipulative experiments, several studies have suggested that when floral characteristics such as color, shape, odor, and handling technique are more distinct, pollinators are more constant (e.g., Bateman 1951; Ostler & Harper 1978; Pleasants 1980; Waser 1986; Dukas & Ellner 1993). In addition, there are many reports that pollinators tend to be inconstant when flowers vary in only one trait, but become more selective if flowers differ in two or more traits (e.g., Waser 1983, 1986; Gross 1992; Gegear & Laverty 1998; Goulson & Wright 1998).

Increases in these two types of floral-trait variation may affect foraging behavior in very different ways if among-trait variability is more difficult than within-trait variability for pollinators to process, remember, or recall. Psychological experiments on humans and pigeons have found differences in responses to within- and among-trait variability, and these have been explained by a concept known as serial and parallel processing (Nakayama & Silverman 1986; Shettleworth 1998; see also Chittka *et al.* 1999). If a target type is presented simultaneously with other non-target types differing in just one feature (e.g., color), then it is processed in parallel with no reduction in the time taken to pick out this target type regardless of the number of other non-target types present. However, if the target is characterized by two or more variable features (e.g., color and shape), then information on each of the two features is processed serially, which takes longer and is less efficient. An analogous mechanism may account for floral constancy in pollinators. The trait variability hypothesis predicts that pollinators should exhibit floral constancy and preference when the number of variable traits increases, because information becomes more difficult to process. However, the same amount of variation in states within a single trait should be much easier for the pollinator to process and so would be expected to produce less selectivity.

We tested these predictions with naïve bumble bees (*Bombus impatiens*) in a series of 10 separate laboratory experiments in which we systematically manipulated the floral variability within and between floral traits in

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arrays of 80 artificial flowers. Following the methods used by Gegear & Laverty (1998), we first ran discrimination tests on pairwise combinations of the flower types used in each experiment to ensure that the bees recognized the different types. Flowers were constructed from colored Eppendorf centrifuge tubes (1.5 ml), so that floral states and traits could be easily manipulated in a standardized manner. In addition to color, we varied flower size (3 or 6 cm diameter collar around the entrance to the tube), and flower complexity by making it easy (cap on centrifuge tube removed) or difficult (cap blocking most of tube entrance) for bees to crawl into the tube. Table 1.1 summarizes the combinations of within- and among-trait variability, as well as the flower types used in each experiment.

Test bees were pretrained to complete foraging trips on several different pure arrays of single flower types, presented in random order, to ensure that they had fully learned to work each flower type. On the day of testing, each test bee completed one foraging trip on each flower type to be tested. Each bee was then tested on a mixed array of 80 flowers with equal numbers of each flower type arranged equidistantly and containing equal rewards (2  $\mu$ l of 30% sucrose solution, refilled after each visit). The first 100 flowers visited by each bee in the mixed array were videotaped for later analysis. Separate groups of 10 bees were run in each experiment; 100 bees were tested in total. We measured these response variables: preference of each bee for a particular flower type on the mixed array (tested by comparing the total number of visits to each flower type using a  $\chi^2$  test); and, flower constancy of each bee (comparing number of moves to flowers of the same type, “like-like” moves, to the number of moves between unlike flower types in the visit sequence on the mixed array using a  $\chi^2$  test). In addition, we quantified flower constancy of all 10 bees in each experiment using Bateman’s Index (Bateman 1951). This measure, ranging from  $-1$  (inconstancy) to  $+1$  (complete constancy), summarizes the tendency of foragers to move sequentially among the same flower types. We used regression analysis to test if the above three variables increased as the number of states within a single trait was increased from 2 to 4 (Experiments 1–7) and also as the number of variable traits was increased from 1 to 3 (Experiments 1–10).

Within experiments, there were no consistent biases in the flower types visited by bees but the percentage of bees showing selective behavior (preference and constancy) varied considerably among different



Table 1.1. *Floral traits, state of each trait and number of flower types used in Experiments 1–10.*

Experiment	Traits varied	States varied	N <sup>a</sup>	Flower types in each experiment <sup>b</sup>
1	Complexity	Easy (open entry) Difficult (closed entry)	2	 
2	Color	Yellow Blue	2	 
3	Size	Small (3 cm diameter) Large (6 cm diameter)	2	 
4	Color	Blue Orange Purple	3	  
5	Color	Yellow Blue Purple	3	  
6	Color	Yellow Blue Orange Purple	4	   
7	Complexity	Easy Difficult	4	   
8	Color	Blue Yellow	4	   
9	Complexity	Easy Difficult	4	   
	Color	Blue Yellow		
10	Size	Large Small	8	   
	Color	Blue Yellow		
	Complexity	Easy Difficult		

Notes:  
<sup>a</sup> Number of flower types in mixed array.  
<sup>b</sup> Flower symbols illustrate different flower types. (Color: clear = blue; striped = yellow; hatched = orange; checkered = purple; Complexity: open = easy; closed = difficult; Size: small = 3 cm; large = 6 cm).

experiments. Bees increased their selectivity as the number of variable traits increased from 1 to 3 in different experiments (Fig. 1.2). All three response variables showed the same trends. As among-trait variability increased, more bees showed preferences for some of the flower types available (Fig. 1.2a,  $F = 8.14$ ,  $df = 9$ ,  $p = 0.021$ ,  $r^2 = 0.50$ ); also, our measure of constancy increased (Fig. 1.2b,  $F = 15.88$ ,  $df = 9$ ,  $p = 0.004$ ,  $r^2 = 0.66$ ) and Bateman's Index approached +1, indicating that moves among flowers of the same type were increasingly common (Fig. 1.2c,  $F = 31.51$ ,  $df = 9$ ,  $p = 0.0005$ ,  $r^2 = 0.80$ ).

In contrast, increased variation within states of a single trait (Fig. 1.2, 1–4 states of one trait) did not increase preference (Fig. 1.2a,  $F = 0.0006$ ,  $df = 6$ ,  $p = 0.98$ ,  $r^2 = 0.0001$ ), constancy (Fig. 1.2b,  $F = 0.01$ ,  $df = 6$ ,  $p = 0.92$ ,  $r^2 = 0.002$ ), or Bateman's Index ( $F = 0.04$ ,  $df = 6$ ,  $p = 0.57$ ,  $r^2 = 0.07$ ).

The observed increase in selective foraging behavior is not explained simply by increases in the number of different flower types learned – this is clear from the behavior of bees in experiments testing the same number of flower types. In arrays with 4 flower types, variation within a single trait (4 colors, Experiment 6; floral complexity, Experiment 7) provoked less constancy than the same amount of variation among traits (color and complexity, Experiment 8; color and size, Experiment 9; Fisher's exact test,  $p < 0.05$ ).

Are these patterns of selective foraging behavior consistent with Darwin's hypothesis or the search image hypothesis? Darwin's idea predicts that bees should be constant only when there are costs associated with switching among flower types differing in handling methods. Because bumble bees experience negligible costs associated with switching between two different handling methods (Laverty 1994b; Gegear & Laverty 1998), bees were not expected to display constancy in any experiment. Although bees did forage randomly when flower types differed only in complexity, bees were constant when flowers varied in more than one trait. In addition, bees were constant in several experiments that did not involve variation in complexity. When bees are presented with multiple floral signals, the search image idea predicts that individuals should focus on one floral feature (e.g., yellow color) and restrict their visits to flowers with similar features. Some bees tended to show constancy to color in some experiments, but most did not do so in experiments in which color alone was variable. The observed patterns are not accounted for by either hypothesis.