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Flower Constancy, Insect Psychology, and Plant Evolution

Lars Chittka[1], James D. Thomson[2] and Nickolas M. Waser[3]

[1]Zoologie II, Biozentrum, Am Hubland, D-97074 Würzburg, Germany
[2]Ecology and Evolution, State University of New York, Stony Brook, NY 11794-5245, USA
[3]Department of Biology, University of California, Riverside CA 92521, USA

Individuals of some species of pollinating insects tend to restrict their visits to only a few of the available plant species, in the process bypassing valuable food sources. The question of why this *flower constancy* exists is a rich and important one with implications for the organization of natural communities of plants, floral evolution, and our understanding of the learning processes involved in finding food. Some scientists have assumed that flower constancy is adaptive per se. Others argued that constancy occurs because memory capacity for floral features in insects is limited, but attempts to identify the limitations often remained rather simplistic. We elucidate now different sensory and motor memories from natural foraging tasks are stored and retrieved, using concepts from modern learning science and visual search, and conclude that flower constancy is likely to have multiple causes. Possible constraints favoring constancy are interference sensitivity of short-term memory, and temporal limitations on retrieving information from long-term memory as rapidly as from short-term memory, but further empirical evidence is needed to substantiate these possibilities. In addition, retrieving memories may be slower and more prone to errors when there are several options than when an insect copes with only a single task. In addition to memory limitations, we also point out alternative explanations for flower constancy. We then consider the way in which floral parameters, such as interplant distances, nectar rewards, flower morphology, and floral color (as seen through bees' eyes) affect constancy. Finally, we discuss the implications of pollinator constancy for plant evolution. To date there is no evidence that flowers have diverged to favor constancy, although the appropriate tests may not have yet been conducted. However, there is good evidence *against* the notion that pollinator constancy is involved in speciation or maintenance of plant species integrity.

Only the honeybee with its highly developed brain has managed to be programmable for only a single (floral) species.
Ruttner 1993 [1] (translated by the present authors)

These bees were a little more highly intellectual than their fellows, and could manage to work the two species together, although I should fancy more than two would puzzle them.
Christy 1884 [2]

The ecological meaning of flower constancy is easy to see for the plants as well as for their visitors. Constancy gives the flowers their only chance to be pollinated with a sufficient amount of conspecific pollen....
Kugler 1943 [3] (translated by the present authors)

Honeybees were so constant to color that behavior could effect sympatric isolation in a color-dimorphic plant species.
Wells and Wells 1985 [4]

Sympatric origin of floral isolation by... flower constancy has been proposed, but... (is) undocumented and improbable.
Grant 1994 [5]

Introduction

A pollinator flying through natural habitats typically encounters several dozen plant species in flower. In a single small meadow in which we collected data on bumblebee foraging [6] an insect flying as slowly as 50 cm/s encountered an average of seven inflorescences from up to five plant species per second (based on a visual resolution of 5° and the assumption that all inflorescences are 3 cm in diameter). In other words, the insect's eyes "report" detection of an inflorescence every 0.14 s. Every time this happens, the insect must compare such input from its visual periphery with previously stored memories of flower signals and their rewards to differentiate familiar rewarding flowers from familiar unrewarding ones and from unknown flowers. This is a tall order, and, unsurprisingly, many insects resort to a strategy to keep it simple: individuals often specialize on only a few or a single species [7]. Different members of the same insect species often forage from different plant species. While searching for those favorites, such individuals ignore the flowers of other species, even if these are equally or more rewarding [8, 9]. The question of whether this *flower constancy* is adaptive has long been debated.

To some scientists, flower constancy seemed to reflect an ability to *learn* floral features, such as their colors, odors, and patterns, and to use these as predictors of floral reward [10]. Visits to species other than the present specialty appeared to these scientists to be errors, in which an insect confuses the other species with what it currently "should" be visiting. In this view, flower constancy is a particularly smart strategy (see Ruttner, above). This explanation, however, is puzzling for scientists familiar with optimal diet models. Such models assume that movement distances between food sources should be kept to a minimum [11]. For this reason, and because there is seldom a single best food source, the optimum diet is often a mixture of several food types [12]. Specializing on any one flower type, and skipping other valuable ones that are encountered *en route*, is not a strategy to maximize energy intake per unit time [7]. A resolution between these two schools of thought seems to be this: if insects visit only a single flower species (and if we can exclude that this is because of an innate preference), such flower constancy clearly involves learning. If an insect visits more than a single species, this can mean either that it remembers *all* the species involved, or that it is able to remember *none* of the species.

These two possibilities are distinguishable. Whether insects can skillfully locate and handle the flowers of distinct species, rather than randomly choosing, is testable. Since Waser [7] pointed out that flower constancy might be explained by constraints of memory, a series of studies has explored whether and how insects can cope with several tasks. Substantial data have now been collected showing that there can be decreases in efficiency when insects execute more than one foraging task. However, the memory mechanisms involved in these phenomena are still not fully understood, although large advances have been made in recent years in identifying neural and molecular mechanisms of learning and memories in honeybees, particularly by Menzel and his coworkers [13–15]. Many behavioral ecologists, nevertheless continue to ignore these advances. Studies often treat memory as a single, unstructured "space" in the head of an insect, which either is or is not large enough to hold the properties of more than one flower species. To determine whether repetitive flower visitation is adaptive, we must distinguish between (a) different kinds of memories, such as sensory memories (in which the colors, patterns, and odors of flowers are laid down) vs. motor memories (which contain the information on how flowers are manipulated to extract rewards in a most efficient manner); (b) different temporal forms of memory [e.g., short vs. long-term memory); and (c) effects during storage (when an insect first familiarizes itself with one or more novel flower types) and in retrieval (when memories are already established but need to be "uploaded", either repetitively, or alternatingly). These processes can have very different temporal properties; they differ in terms of the neural substrate employed [13, 15] and potentially in their capacities [16].

Flower constancy has obvious implications for the evolution of plant sexual signals because it facilitates pollen transfer between conspecifics (see Kugler above). Conversely, pollinators straying between flowers of different species may lose pollen during interspecific flights [17, 18] or clog stigmas with foreign pollen [17, 19, 20]. Inconstant visitors may also depress floral reward levels, thus discouraging more efficient pollinators [21]. In some closely related species, hybrids may be produced which are sometimes less viable than the parental species [22]. Some authors have imagined further that constancy was actually involved in speciation of plants [23]. Flower constancy has also been implicated in the maintenance of plant species integrity [24, 25]. An alternative view, which we are led to, is that pollinators are rarely so constant that they will strongly isolate two morphs of the same species reproductively.

Memory Limitations that Might Favor Constancy

STM, LTM, Working Memory, and Reference Memory

From mollusks through insects to mammals, animals have distinct temporal forms of memory, traditionally referred to as short-term and long-term memory (STM and LTM) [13, 26, 27]. Knowing the capacity and temporal dynamics of these forms of memory in insects is central to understanding whether flower constancy can be explained by memory constraints. STMs are short lived (usually from seconds to minutes) and volatile. They rapidly decay even without interference and can be easily erased by competing information or shock [28]. One's STM is active when reading a new telephone number, dialing it, and then forgetting it. One forgets it even before dialing if someone yells a different number. LTMs last for several days and potentially through the lifetime of an animal and are much more resistant to forgetting. In humans, STM and LTM also differ strongly in terms of their capacity: one can retain several telephone numbers in long-term storage (in addition to much other information), but memorizing several new ones at a time is probably too great a challenge. Much of LTM lies dormant at any one time, and input to (and, in humans, retrieval from) LTM is relatively slow. Human STM keeps information in an active state, swiftly stores new information, and allows rapid retrieval [16]. STM involves the temporary activation of neural circuitry [15], which can be sustained for some time by recurrent activation [29, 30]. LTM requires long-lasting changes in the structure of neural networks.

Traditionally, STM has been considered the gateway to LTM, bridging the time until LTM is established [10]. However, at least in mammals, STM can receive input not only from the outside world but also from LTM [29, 30] (most readers can probably "upload" their penultimate phone number from LTM and, once it is in an uploaded form, are able to retrieve it more rapidly). Separately stored pieces of information can be combined in STM and be used in novel adaptive ways [29, 30]. STM is also involved in selective attention to particular stimuli. In fact, in primates the mechanisms for STM and attention are so intertwined that some authors question whether they are distinct [31]. In this view, attention to a particular stimulus is mediated simply by keeping previously stored information in an active "on-line" state, and incoming stimuli then interact with information in that active state. Many authors now use the term "working memory" instead of STM, and "reference memory" instead of LTM [16]. Others use "working memory" only in cases when the brain "brings to mind" earlier memories in the absence of direct stimulation [29]; yet others use "working memory" for STMs of particularly short duration and with less specific content [15]. We use the traditional terminology of STM and LTM throughout this review. In bees the dichotomy of STM vs. LTM is slightly simplistic because there are multiple successive memory stages with durations of seconds, minutes, hours, days, and possibly weeks. (For an excellent recent survey see [15].) We categorize here as STM those forms of memory which are sustained in the seconds to minutes range, and as LTM those memories which are kept for hours and above.

LTM Capacity in Bees Is too Large to Explain Constancy

The relevance of STM and LTM for foraging has been little considered (for exceptions see [13–15, 32]). Indeed, some authors have claimed that bees have no LTM (e.g., [33])! This claim is untenable. The two insect model organisms whose memory has been studied in detail (the fly *Drosophila melanogaster* and the honeybee *Apis mellifera*) have STM and LTM with many of the characteristics described for mammals above [15, 27]. A simple explanation for flower constancy would be that insects are able to memorize only how to handle or identify a single species at a time. However, LTM capacity, at least in bees, is frankly astonishing. Bees must store large amounts of spatial information, such as the location of the nest and of flower patches, as well as their position relative to surrounding landmarks [34]. The number of such landmarks that can be stored is at least six, and the bee can link these to specific routes that guide them to various food sources [35]. Honeybees form long-term expectations of rewards to be expected at individual artificial flowers, at least when the number of flowers is small [14]. Bumblebees can remember individual plants in a large array, and visit such plants in a statistically repeatable sequence, a *trapline* [36].

Obviously, bees must also remember the sensory stimuli that are associated with floral rewards. Once stored in LTM, such memories are retained for several weeks, i.e., practically for the natural lifetime of a foraging worker bee [10]. Kugler [3] was the first to show that bumblebees can be trained to two odors and colors and to distinguish both from unfamiliar ones. Honeybees [37] and bumblebees [38] can distinguish three rewarded stimuli from three unrewarded ones, and some individuals discriminate four positive from four negative stimuli. It is likely that, if flowers are specified by more than a single cue (odor, color, pattern, shape, size, height, place, flowering time, etc.), the number of flowers that can be memorized is even higher. LTMs in bees are not erasable by interference from competing information (such as learning new associations [10]). In summary, a wealth of evidence shows that flower constancy in bees is not caused by strong limitations of LTM, in the sense that bees can memorize only how to locate, identify, and handle one flower species. Much of the LTM contents, however, are dormant at any one time. For example, familiar landmarks which usually mark the feeder may be entirely ignored when they appear at an unexpected location [39]. This is a striking example of a bee not using "dormant" information which we know is stored in its LTM. Only when the bee has already flown close to a site where it expects the landmark is the landmark apparently uploaded into a short-term "search window" that the bee responds to appropriately. When bees are flower constant, they may similarly ignore even familiar flowers which are currently not in an uploaded state.

STM in Insects: Does it Hold the Key to Constancy?

New floral stimuli are first stored in STM which decays after a few minutes [10]. It is also sensitive to interference: if honeybees are given two subsequent learning trials in quick succession with two *novel* different odors or colors, the memory for the first stimulus can be effectively erased [28]. We conclude that two *novel* sensory stimuli cannot be simultaneously held in STM. This suggests that constancy should be favored during learning of novel stimuli, or bees should try to avoid the critical time intervals when interference is strong. Interestingly, when bees are forced to switch between two novel flower types with distinct colors, but are given free choice as to the time interval between trials, they do exactly that: whereas transitions between identical flower types took 30 s in an experimental array, bees waited 100 s before visiting a flower of a different type. Once bees had learned the tasks, transitions between different flowers were as rapid as between same flowers [40].

Each time a flower is visited, the traits that characterize this flower reactivate the STM for these traits. If, as in mammals, the contents of STM are more rapidly retrievable than are those of LTM, bees can react to a flower of the same species (as the one just visited) more swiftly than to another flower whose sensory traits must be uploaded from LTM [6]. In other words, the bypassing of flowers of other species observed during constancy does not show that bees remember only the flower type last visited. Rather, the flower type last visited is simply the one that is most readily retrieved from its memory. Results from field observations are consistent with this interpretation. In the first few seconds of flight after a floral visit, the probability of visiting another flower of the same species is exceptionally high, even when other flowers are available at closer distance [6]. As more time passes during flight, bees become more ready to accept alternatives. In such cases, even if insects switch to another *familiar* species, we suspect that they must browse their LTM library for the signals that characterize those species, which takes more time than to compare visual input with information that is currently in an active STM state. However, more experimental data are needed here.

The evidence from experiments in which bees learn *novel* stimuli suggests that STM can hold the properties of only a single flower (see above). But does this really mean that bees can only search for one flower type at a time? In one study, bees foraging in meadows that contained several flower species readily accepted alternative flower species when offered a choice between the flower species last visited, and another that it likely had recent experience with. Conversely, bees that foraged in monospecific meadows are often more flower constant when offered choices [41]. One interpretation is that bees in mixed floral arrays actually hold more than one flower type in an activated STM state. Therefore they may respond more readily to flowers which differ from the one last visited. When a familiar flower has not been encountered for a critical time, it fades from STM; thus, the next time the information for that flower is needed, it must be uploaded from LTM. Clearly this scenario is speculative and needs further experimental exploration.

It is also important to keep in mind that, as in mammals [26], insects have several forms of STM, which differ in their decay times and their contents [15]. In addition to short-term storage systems for the sensory stimuli that characterize flowers, another STM system is used for path integration; this allows bees to update continuously all distances traveled and angles turned so as to keep an update of the direction home [34]. The information is constantly replaced from one instant to the next. This is not the case with all STM information. In an elegant experiment in which bees foraged among four artificial flowers with variable rewards, bees were able to retain the information of the last reward at each flower at least until the next time the same flower was visited, even if other flowers had been visited in between [42]. A further STM process is active when bees choose flight directions after each flower visit. Bees generally move straight ahead when recently encountered flowers were poorly rewarding, and in sharp angles after having found a high reward, which improves the probability of staying in rich patches [9]. For this strategy to work, bees must remember the direction of arrival at a flower. Understandably, this information is not stored in LTM for the hundreds or thousands of flowers visited during a foraging bout – instead, it is replaced rapidly as the bee moves along its foraging path [43]. Note, however, that when bees forage extensively and for long periods of time in a single floral array, the rough geometry of a foraging flight may become increasingly repetitive [36], certainly using long-term landmark and flight vector memories [34].

Several STMs are usually simultaneously active, and thus there is not necessarily a trade-off between different activities (such as choosing food and remaining vigilant for predators), as some authors have suggested. We wish to emphasize the fact that, while the ability to keep several memories active is surely more limited than the total ability to store information, foraging insects are certainly able to juggle substantial amounts of information efficiently.

What are the conclusions for constancy? First, and particularly during learning of novel flower types, the interference sensitivity of STM may explain why bees temporarily specialize on single flower types. Once familiar with the flowers, a bee may be able to retain more than a single flower in STM. However, familiar flowers which have not recently been visited are no longer in an activated state. In this case the bee needs to scan its LTM, which implies a time delay. Thus constancy may be in part an effect of temporal limitations on information processing rather than of capacity. Because all previously stored information is not equally readily available, bees may be more likely to visit flower species that have been encountered in very recent foraging history.

Limitations of Motor Learning?

In addition to learning the sensory stimuli that characterize a flower (such as odor and color), flower visitors must learn particular motor patterns needed to harvest nectar and pollen. While some flowers have simple morphologies, others demand complex handling procedures, which involve prying petals apart (horizontally or vertically), inserting the head in a particular direction, and extending the proboscis into long spurs [44].

Even bees that are genetically predisposed to forage from only a single species of plant show considerable improvement from early to late trials on their floral specialty [45]. In generalists the need to learn how to forage from various plant species is even more obvious. Thus, unsurprisingly, bumblebees [40, 44] and butterflies [46] are able to learn how to handle a large variety of flowers. Naive insects are clumsy: in complex flowers (natural or artificial), they require five to ten times the handling time of an experienced forager, and sometimes need a full minute to exploit a flower [40, 44]. A saturation level of efficiency is reached even in complex flowers after about 100 trials. When bees learn to handle a novel species whose morphology is similar to one previously learnt, *positive transfer* occurs, and bees do not start out as poorly on the new species as does an entirely naive forager [40, 44].

Memory capacity has not been explicitly tested, but bees can certainly memorize more than a single handling procedure. We observed bumblebees foraging proficiently from five different flower species without increased handling times after species switches [6]. In the laboratory, bumblebees learn to forage from artificial flowers with two distinct morphologies, although not as efficiently as on a single flower (see below; [40]). Handling procedures are retained in LTM for more than 3 weeks, although some decay occurs [47].

Does learning to handle a novel species interfere with the knowledge to handle previous ones? Interference occurs when subjects are trained first on one task and then on a second, and the memory for the first task is erased (or weakened) by training on the second task. Interference in learning how to handle flowers has been frequently cited as a likely cause for constancy [46, 48], and interestingly, most authors cite "Darwin's interference hypothesis" in this context [49]. However, Darwin actually did not claim that the memory for one task is weakened or erased when a new one is learnt. He said [50]:

"That insects should visit the flowers of the same species as long as they can, is of great importance to the plant, ...but no one will suppose that insects act in this manner for the good of the plant. The cause probably lies in insects being thus enabled to work quicker. They have just learnt how to stand in the best position on the flower, and in how far and in what direction to insert their proboscides. They act on the same principle as does an artificer who has to make half a dozen engines, and who saves time by making consecutively each wheel and part of them."

This statement stops somewhat short of explaining flower constancy, because having learnt how to stand in the best position on one flower type, does not, *a priori*, prevent insects from learning how to stand in the best position on another. In addition, the memory of Darwin's artificer is clearly not constrained to perform only a single task. The artificer does not forget how to make wheels while he is making other parts. Yet, he is apparently more efficient when he executes the same task repetitively, rather than switching randomly. Is the same true for flower visitors, or is there evidence of interference in insect motor learning?

One prediction from interference would be that insects exhibit longer handling times immediately after switching from one species to another. Laverty [48] tested this prediction and found no such increases when bumblebees switch between morphologically simple flowers, and (statistically weakly significant) increases of about 1 s after switches between complex flowers [48]. Similar costs were described in butterflies [49]. Even though these costs are small, they may add up to a substantial decrease in foraging gains over the lifetime of a flower visitor. However, the increases in handling times after switches are 10–50 times lower than are the handling times exhibited by naive insects. Thus insects clearly had not lost the LTM of handling one flower species while visiting another. Nevertheless the described offsets in handling time may be a consequence of delayed retrieval from LTM, as we earlier described in sensory memories. If a flower has not been handled for a critical amount of time, the motor memory may be lost from STM, and the insect may have to scan its LTM for the appropriate handling procedure, which takes more time. The same explains why humans (such as Darwin's artificer) are more efficient when performing the same task repetitively, rather than alternating at random intervals [51]. Alternatively, the delays after switching may be a result of STM interference (i.e., the active memory for handling one species is replaced by the active memory of how to handle another, without interfering with LTM), but the field experiments described above do not allow us to distinguish between passive decay and active interference.

There is one report on *Pieris* butterflies, however, in which learning to handle a second flower species seems almost completely to erase the memory for the first [46]. This could in fact mean that LTM in *Pieris* is so limited that it holds only a single handling procedure. Alternatively, however, such interference might be caused by a particular training schedule. The butterflies were trained in a blocked schedule. This means that they first learnt task 1 with several consecutive trials, until saturation was reached, and then task 2 in the same way. It is well known in human psychology that blocked training schedules are inefficient for storing distinct motor tasks. Subjects trained with mixed schedules are somewhat slower in the learning phase, but substantially superior in efficiency and accuracy in later trials: the "contextual interference effect" [51]. To test for this effect in bumblebees, we trained them in two artificial flower types with distinct morphologies. As in real flowers, bees had to use colors of the flowers to predict which motor patterns were appropriate [40]. One group was trained in a blocked schedule with 100 trials on one task and then 100 trials on the other task. The second group also received 200 trials total, but had to alternate continuously between tasks. Afterwards, bees of both groups were tested on both tasks. The result was striking: in the test phase bees trained in a blocked schedule were initially incapable of coping with the task learnt first, whereas bees trained with a mixed schedule dealt with both tasks appropriately. Thus interference may occur when insects learn to handle two or more flower types with many consecutive trials. There was an additional important effect, however: bees trained with a blocked schedule apparently did not learn to associate flower color with motor pattern. They simply learnt to use the same motor pattern in all flowers, and replaced this motor pattern with another when they learnt the second task. In other words, they failed to establish the context which specified the correct motor pattern in each flower type. Thus inconstancy may have a beneficial effect in the learning phase: bees that switch between tasks may be better able to learn associations between the sensory stimuli of flowers and the particular motor patterns needed to extract the nectar. However, this increase in learning efficiency takes place only if bees avoid the critical time intervals when STM interference occurs (see above).

A different effect is found in the saturation phase, when bumblebees are already familiar with their respective flower handling tasks. We found that bees trained on only a single task performed this task with high accuracy and efficiency. They made practically no errors (attempts to use the wrong motor pattern to reach the nectar) and handled flowers more rapidly than did bees trained on two tasks. Bees trained on two tasks did make a substantial numbers of errors (around 8%), and this error score did not approach zero even after several hundred flower visits. Handling times were also drastically longer than in bees which had learnt only a single task (on average 30%, or 3 s longer). Both effects were independent of switch frequency: we forced bees to switch tasks after every visit every 5th visit, every 10th visit, and at random intervals, but the error scores and handling times remained the same [40]. Two explanations are possible: (a) either efficiency and accuracy decrease with an increasing number of options that an insect has stored in memory, or (b) bees that learn more than one flower handling task learn different kinds of tasks. "Single-task bees" apparently fail to associate floral signals with appropriate motor patterns, but simply learn pure motor patterns which they execute "automatically"; therefore the task that they learn is a pure motor task. They must still learn the floral signals to recognize their flowers, but apparently not to retrieve the correct motor pattern. Conversely, bees which learn several tasks learn sensorimotor tasks (associations of sensory signals with motor patterns). They must scan their memory for the correct motor pattern, which may impose delays.

What are the implications of these results for temporary task specialization in insects? Flower constancy appears to be the optimal strategy when the described limitations of sensorimotor memory retrieval are taken into account. The best performance is reached by animals that focus on a single task. They make practically no errors and are fast at correcting the few errors that they make. It is possible, however, that inconstant insects are more efficient and accurate when more contextual cues are available than merely flower color. For example, if the flowers in our study had had different shapes and scents, or if they had been located in different places or available at different times, our "dual-task bees" might have performed better.

Flower Constancy and Visual Search

There is an extensive literature on human capacity limitations, time constraints, efficiency, and accuracy in picking a given number of defined objects from a larger sample; the field is called *visual search* [31, 52]. Interestingly, the common tests run by psychologists seem more appropriate to a bee's world than to a human's. Subjects are commonly asked to search a computer screen for one or several defined targets (such as a small blue star). The targets may either move across the screen from the periphery or appear at certain locations in the center of the screen, and they are commonly mixed with other stimuli (distractors) which differ from those the subject is asked to search for. Targets may differ from distractors in one stimulus dimension only (such as color), or they may differ in several dimensions (such as color and shape). Performance of subjects is evaluated in terms of reaction time and accuracy, and in terms of the individual strategy used to optimize the speed-accuracy tradeoff [53]; possible errors include "false alarms" (reactions to distractors), "missed targets" (the subject fails to react to a presented stimulus [53], and premature abortion of search in a particular area [54]. Notice the similarity here with an insect searching a meadow for familiar rewarding floral signals, and making mistakes along the way!

The visual search literature is full of exciting discoveries with relevance for foraging animals. For example, when there is only one target type, there appears to be no decrease in efficiency with an increasing number of different distractors, so long as stimuli vary along a single parameter (i.e., they all have the same shape, but differ in color). In such cases subjects examine all presented stimuli in*parallel*, the target is said to "pop out," and the reaction is accordingly rapid (parallel search). If, however, targets and stimuli vary along more than a single dimension (e.g., color *and* shape), each stimulus is examined in series (serial search). In this case reaction times increase drastically with the number of distractors [55]. Reaction times may also increase with the number of targets simultaneously sought [56]. Reaction times are longer when subjects have no prior expectation of where a stimulus might occur than when it occurs at a location where they expect it. They are even slower when subjects expect the stimulus at a certain place, but it actually appears somewhere else [52]. Both speed and accuracy depend on the similarity of targets and distractors [57] as well as the similarity between target and background [58].

These findings, should they prove valid for pollinators, have obvious implications for flower constancy. Unfortunately, scientists studying animal behavior often implicitly assume that animals can attend to only a single task at one time, and tests are sometimes designed so that a decrease in efficiency with an increasing number of tasks is the only possible result. In one study [59] bees were tested in their ability to distinguish one, two, or three rewarded targets with different colors from a nonrewarded distractor (in the terminology above). The bees made mistakes (visits to the unrewarding stimulus) more frequently when there were more rewarded targets in the array. This effect, unfortunately, may have been an artifact of the training procedure: the number of opportunities to learn each stimulus type was inversely proportional to the number of stimulus types used. To choose each stimulus with a given accuracy the bee should ideally have been given an equal number of rewarded trials on each such stimulus prior to testing. But this study is certainly a step in the right direction!

Alternative Explanations of Constancy (in Addition to Memory Limitations)

The Learning Investment Hypothesis

The citation from Darwin given above refers not only to an artificer but also to the possibility that flower constant insects "... have just learnt how to stand in the best position on the flower, and in how far and in what direction to insert their proboscides...." This statement has been taken by several workers to mean the same thing as the "artificer argument," which we discussed above in terms of a time cost of retrieving information from LTM. However, we take Darwin to mean something different here. Darwin's artificer had to learn his skills at some point, but how can such learning explain why he is more efficient when he manufactures different components repetitively? As we noted above, a possible interpretation is that learning a motor skill requires such substantial investments into learning that switching is inherently maladaptive. However, the time costs of learning to handle novel flower species have now been quantified [40, 44], and they appear to be too small to substantiate this supposition. Depending on floral complexity and previous experience of the insect, learning to manipulate a new flower species takes between 30 and 100 flower visits, thus consuming less than 1 h of an insect's foraging career [7]. Learning the sensory stimuli of flowers takes even fewer trials: depending on stimulus modality (odor, color, etc.) and insect species, between 1 and 20 rewarded trials are sufficient to reach saturation and establish a LTM that lasts for several weeks [60–62]. Most of these data come from honeybees and bumblebees, but solitary bees [63], butterflies [46, 64], and moths [65] appear to be similar.

To us, the most parsimonious interpretation of what Darwin meant is simply this: learning to handle one flower type makes the insect more efficient on that flower type than on any other flower type that it is not familiar with. Insects may be resistant to switching from one plant species to an unfamiliar one because the novel activity invariably involves a phase of poor efficiency. Thus the new activity yields lower immediate gains for an intermediate period. During this period the insect may have no way to determine whether the value of a novel flower type is poor because indeed there is only a small reward in it, or because the insect is inefficient at extracting this reward. Consequently the insect may prefer to switch back to its previous flower species (or stay with it in the first place). In other words, the same mechanisms that make an insect forage efficiently may lead to a certain inertia in switching tasks.

The insect faces an additional problem: it cannot predict the outcome of its venture to a novel flower species. The best that it may be able to do is to use a memory of past learning to predict how long such learning will take in the future. If so, an insect that took a long time to learn the motor pattern to handle a species in the past, for example, because it picked a very complex flower species, may be less ready to switch to any other flower species, independent of its complexity. In conclusion, what Darwin might have meant is not that bees are inherently too *constrained* to perform several tasks, but rather too *cautious* to switch to a new activity when this involves a phase of poor performance. We view this hypothesis as fundamentally different from the simple "cost of switching" argument discussed earlier, because it revolves around the insect's imperfect *a priori* knowledge of the handling times and techniques of different flowers. The hypothesis makes a testable prediction that insects constant to complex flowers should be more reluctant to switch than those constant to simple flowers.

The "Costly Information" Hypothesis

Some authors have suggested that foraging insects are generally constant except when they sample alternative flower species that are potential targets of future specialization [9]. This is not the whole story, because insects often do forage from more than a single species systematically [6]. However, sampling certainly also contributes to inconstancy. In general, we expect an optimal forager to divide its time in some way between collecting food at familiar sources and collecting information about alternatives [66]. On the other hand, when the collection of new information is prohibitively costly in time and energy, the forager may avoid doing so and be highly constant.

Nectar or other rewards are variable from flower to flower and plant to plant of a single species. It may simply be most efficient for the insect to sample until it finds a plant species with rewards above a certain threshold of acceptability, and then remain constant as long as that species is available. Doing otherwise, for example, attempting to visit different flower species depending on their expected rewards [67], may involve an excessive investment toward gaining accurate information and may actually yield a lower final foraging efficiency. The crux of the issue is how many flowers the pollinator must sample to obtain a good estimate of a new plant's mean value and thus to determine whether it is equal, worse, or better than the one(s) currently visited. If this number is large, the cost of sampling may be prohibitive and the pollinator remains constant. The answer depends on the variance in reward among flowers of the novel species. To estimate how many flowers must be visited it is helpful to recall sampling theory. Regardless of the form of the probability distribution of rewards, the means of successive samples of size N will be approximately normally distributed (by the central limit theorem), with the grand mean equal to the expected value of the reward. The standard deviation of the mean is estimated by the standard deviation of rewards in a single sample, divided by the square root of N. Thus, if a bee, for example, samples N flowers, the sample mean is her best estimate of the expected reward for the species. However, her estimate of the mean becomes more precise as N increases. To double the precision (to halve the confidence interval around the mean) requires a fourfold increase in N. The conclusion is that the necessary sample of flowers or plants must grow rapidly to gain more precise information of the expected reward.

Consider an example based on the actual measured values for nectar rewards. If *Delphinium nelsonii* flowers in a population have a mean nectar volume of 0.5 μl and standard deviation of 0.38 μl [68], what sample N must a bee take to ensure that the actual mean volume is within 10% of the sample mean with 95% certainty? This corresponds to 0.05 μl being within 2 standard deviations of the actual mean, or twice the sample standard deviation divided by the square root of N. Solving this equivalence yields $N = 231$ flowers that must be sampled for this degree of precision in estimating the actual value of *D. nelsonii* flowers – a large number! Because bees are not statisticians, and are likely to use rules of thumb, they may not do even as well as our calculations. All of this suggests that the costs of sampling can be large, as may therefore be the value of flower constancy.

A testable prediction is that, as the costs of sampling increase, the degree of flower constancy may also increase. In other words, the more unpredictable the environment, the more bees should be faithful to species which they have experienced as rewarding. To our knowledge, this prediction has not been explored. Another hypothesis is that, if information is costly, social bees that communicate about food sources behave differently than solitary foragers. Information gathering in honeybees, for example, is performed by a few specialized foragers (scouts), who transmit their findings to foraging workers. Each forager might then be simply be constant to a species it has been informed of, until further notice. There are ample reports on honeybees being more constant than are, for example, bumblebees (e.g., [69]), but there are problems with these reports. First, contrary to popular belief, bumblebees do have a communication system that informs recruits of the time of flowering of valuable food sources, as well as their odor, so that the plant species is identifiable [70]. Second, most estimates of constancy have been made by evaluating the species in pollen loads carried by bees. Honeybees have seemed to carry more pure loads than bumblebees. However, pollen loads are a poor indicator of constancy because plants are often clustered in space, and pure pollen loads may therefore indicate constancy to a place, with constancy on a species as an epiphenomenon. This is a critical limitation of all but the most recent assessments of constancy [7, 71]. There really is no option but direct observation of foraging behavior when we know that the insect has more than a single plant species from which to choose. Surprisingly, comparative studies of constancy in various insect species at the same time and place, with the same array of flowers from which to choose, are almost entirely lacking. A fairly old study [72] which meets these requirements found that honeybees are more constant than bumblebees, and bumblebees more constant than unspecified species of solitary bees. This is in agreement with the hypothesis that communication in social foragers is linked to constancy, but clearly more data are required. Even strictly solitary foragers such as flies and butterflies [49, 73] exhibit constancy, but at present we do not know whether they are more or less constant than social foragers.

The Resource-Partitioning Hypothesis

An entirely different explanation that has been proposed for constancy is that, in social foragers, it is a particularly adaptive strategy for resource partitioning [8]. In this view, members of a colony avoid competition with one another by each specializing on different plant species. In conjunction with strong limitations of memory, this assumption would make sense: if each individual experiences high costs of switching between plant species, foraging labor might be most efficiently divided by building a society of individual specialists. However, can resource partitioning alone explain constancy? When plants of different species are mixed, a better strategy than distributing constant foragers across plant species would be to distribute inconstant foragers across space. To minimize flight paths, each forager would exploit only a small portion of a nest's flight range, but forage from all profitable plants in that portion. Conversely, a nest all of whose constant members consistently skip valuable food sources would certainly not forage as efficiently in terms of pollen and nectar returned per unit time. Thus, without assuming constraints on information processing in individuals and in the colony, labor division through constancy does not appear to be inherently adaptive. Are there known constraints that would keep insects from distributing themselves in space in proportion to the profitability of patches? No such constraints seem to exist: each individual bee is equipped with the sensory machinery and memory to evaluate and compare patch quality [14], with strategies to avoid poorly rewarding or recently depleted flowers [43, 74], and with excellent spatial memory [39]. Bumblebees that use small foraging areas are able to detect and move into adjacent competitive vacuums created by removing other bees [75]. In addition, social foragers such as honeybees use a communication system which deploys more foragers to rich patches [76]. The result is usually that the distribution of foragers across their flight range closely matches an ideal free distribution [77, 78]. In conclusion, bees are able to divide up their foraging space in such ways that competition between individuals of the same colony is minimized. In addition, solitary foragers are also often flower constant [49, 73]. Hence resource partitioning seems to us an unlikely explanation for constancy.

Influences of Floral Features on Constancy

The hypotheses outlined above to explain flower constancy lead to several testable predictions about how features of flowers and plants will influence foraging behavior. When floral rewards are large, and flowers of the same and novel species are available at equal distances, foraging insects should be constant to minimize the costs of switching. Conversely, as travel time between flowers increases, or if all flowers are poorly rewarding, the costs of bypassing alternative species may exceed the costs of switching, and inconstancy should be favored. Furthermore, if insects can evaluate the costs of switching, they should be particularly reluctant to switch to species whose morphologies involve high switching costs. As we have already noted, if insects cannot prejudge the costs of switching, they may use the cost of learning their present specialty as a guide, and individuals visiting complex flowers should therefore be less likely to switch than those visiting simple flowers. Finally, a prerequisite for constancy is that the plants of different species are distinguishable by means of their sensory signals (colors, patterns, scents, etc.). Thus, we predict that constancy increases as flowers become more and more dissimilar in display. This applies both for the case in which bees switch between familiar flowers (because accessing more remote memories for a different signal than the one just visited involves more time) and the case in which a bee switches to a different flower because that flower is so similar to its current specialty that it is mistakenly visited.

Spatial Arrangement of Flowers and Constancy

When distances between flowers are large, bees are predicted to be less constant, because travel costs associated with constancy outweigh costs of switching [7]. Unfortunately, we know of no experiments in which bees encountered switching costs (for example, with flowers of distinct handling procedures) *and* in which distances between flowers were systematically varied. However, effects of spatial arrangements of flowers on constancy are also predicted when there are no handling costs involved in switching. First, if the memory for the flower types visited most recently are more readily retrievable than those for other familiar flower types, the probability to switch flower species should be low in the first few seconds after each floral visit, and should increase as the active memory for that flower type fades [6]. Second, if the current reward status of alternative flower species is difficult to assess, insects are likewise predicted to be reluctant to switch when flowers of the same species are available at close range (see "Costly Information Hypothesis" above). Conversely, if flowers of the current specialty are not encountered for a while as a pollinator searches, the costs of further searching may surpass the costs potentially involved in sampling other flowers. Insects should then be more ready to accept alternatives [6].

There are anecdotal [24, 79] as well as experimental [80] reports to show that constancy indeed decreases with increasing distances between plants. Marden and Waddington [80] tested honeybees in arrays of equally rewarding yellow and blue artificial flowers.

They found that when bees are given the choice between a yellow and a blue flower equidistant from the current flower, they predominantly choose a target with the same color as the one just visited. However, when distances are unequal, bees mostly choose the nearest flower irrespective of color. While the latter is clearly advantageous, the former finding is difficult to understand by adaptive reasoning. When flowers are equally rewarding, and both types familiar to the tested bees, there is no adaptive reason to move preferentially between flowers of equal color. In one field study, bumblebees were observed foraging in a mixed meadow of five plant species. Bees consistently searched for about 3–4 s for a flower of the species just visited [6], and only then switched to alternative species. These results suggest that flower constancy varies with the spatial arrangement of flowers, as predicted. They do not allow us to distinguish, however, between the hypothesis that memories for alternative species are not readily available in the first few seconds after a floral visit and the hypothesis that bees are initially reluctant to switch because of unpredictable rewards in alternative flower species. More experiments are needed to decide between these two alternatives.

Some extreme manifestations of inconstancy may occur when animals become very familiar with a small set of plants in a heavily used foraging neighborhood. For example, J. Thomson (unpublished) observed the sequences of plants visited by a single *Bombus flavifrons* worker which had been foraging exclusively in an array of *Penstemon strictus* plants about 100 m^2 in area for 2 weeks (for details see [36]). By the end of these 2 weeks *Penstemon* flowers were becoming less abundant, and this bee was then making about 25% of its visits to six other species, five of which were yellow, pink, and orange Asteraceae (*Helianthella, Solidago, Erigeron, Chrysopsis, Helenium*), in addition to the papilionaceous *Vicia*. During 336 observed visits this bee switched species 140 times! Furthermore, some transitions between species occurred repeatedly at the same points in space, and therefore the inconstant movements became regular features of this bee's trapline. For example, visits to one *Helianthella* were almost invariable preceded by visits to two specific *Penstemon* plants. (For more details see [81]). Our conclusion is that constancy is influenced not only by the distances between plants encountered by insects searching for flowers whose location is unknown but also by the spatial arrangement of familiar flowers as represented in an insect's memory. When bees become extremely familiar with the spatial arrangement of flowers of their foraging area, they may use spatial-contextual cues or serial memories of flight vectors that may help retrieve memories for handling a variety of different plants (at certain points along a trapline, for example). Such context specific retrieval may make switching less costly.

Floral Rewards and Constancy

Another prediction is that constancy is not inflexibly pursued when rewards are low [14]. When recently encountered rewards at one flower species are poor, insects have two options: leave the patch and fly to another patch of the same species, or stay within the patch but switch to an alternative species. Earlier reports showed that bees often fly to a different patch when recently experienced rewards were low, and a different plant species was not available [43]. Recent reports, however, also show that bumblebees [6] and butterflies [49] switch species with higher probability after receiving lower than average rewards. In these studies, however, reward levels were assessed only indirectly, by measuring the handling time of the flowers (using the rationale that within a plant species, handling time per flower is positively correlated with nectar amount [49]).

Flower Signals, Flower Morphology, and Constancy

Insects may experience time delays after switching between different flowers with complex morphologies or between different flowers with distinct colors or scent signals, but not when switching between flowers more similar in morphology and signal. Indeed, constancy has been reported both for flowers differing mainly in morphology [48] and for those differing mainly in color or scent [4, 20, 82]. Time delays in switching between morphologically complex flowers have also been reported [48]. This finding is not universal; in another study with artificial flowers, bees did not show elevated handling times after switches [83]. However, bees that foraged from flowers with distinct morphologies had consistently longer handling times than did bees that foraged from only one flower type. The fact that there are costs of switching between morphologically complex flowers does not necessarily imply that insects actually evaluate those costs, and respond appropriately. Do bees show higher degrees of constancy when the morphology of flowers requires intricate handling procedures? Laverty [48] found that bees are less constant to flowers with simple morphology than when foraging on flower with complex morphology. There are two possibilities why this might be so: bees are less willing to switch *to* a flower with a complex morphology because they can predict the costs of switching to that flower, or they are reluctant to switch *from* a complex flower because they use the flower currently handled to predict how difficult the alternative will be to handle (See "Learning Investment Hypothesis" above). Because Laverty [48] did not give bees the option to switch from simple to complex flowers and vice versa, we cannot yet be sure which of these interpretations explains the bees' reluctance to switch between complex species.

Turning to flowers with different colors, Waser [7] observed bees of several species in arrays of flowers and found that they are more likely to switch if flowers differ neither in color nor morphology than if they differ only in color; more likely to switch if flowers differ in color alone than if they differ in morphology alone; and more likely to switch if flowers differ in color alone rather than in color and morphology together. The importance of flower color for constancy can be best assessed when color differences between flowers are quantified as bees see them. Since modeling such differences is now possible, we [6] correlated bee-subjective flower colors with constancy levels of foraging bumblebees and found that, indeed, bees switch more frequently between similar flowers and less frequently between flowers whose colors are distinct. In another study based on bee-subjective colors, Wilson and Stine [41] reported that "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." In conclusion, colors may sometimes be even more important than morphological differences between flowers in influencing constancy. This means that flowers of sympatric species becoming more and more dissimilar in small evolutionary steps should indeed favor constancy and therefore a more directed pollen transfer.

Overall, these results support the prediction that constancy is enhanced by differences in handling criteria of flowers and in the visual signals that the flowers send. Finally, some floral signals may be so attractive that they can influence pollinators to be significantly inconstant. In unpublished dual choice trials, J. Thomson found that bumblebees foraging in stands of *Penstemon whippleanus* were more likely to move to a flower of *P. strictus* than to the familiar *P. whippleanus*. These bees had never seen *P. strictus* before. They probably treated them as the same species and were influenced by the greater size of *P. strictus* flowers, and the resulting better detectability.

Flower Constancy and Plant Evolution

Have Flowers Evolved To Favor Pollinator Constancy?

It is hard not to invoke natural selection to explain the great phenotypic diversity that we see in a meadow of flowers. Because many pollinators tend to move less frequently between flower species whose signals are distinct [4, 6, 7, 20, 25, 41], one possibility is that selection has favored divergence of flower signals because this increases constancy [9, 84]. Pollinators switching between flowers may encounter decreases in efficiency and accuracy [40, 48]. If the fitness costs to plants of pollinator switching are large enough, mutants with morphologies or signals that elevate costs to the pollinators may be favored, thus discouraging switching. Not all such divergence would necessarily have occurred in sympatry. It is also conceivable that a novel invader colonizes a habitat more successfully if it fills a "signal niche" that it is not yet occupied, and therefore particularly recognizable for pollinators [20].

It is interesting to compare the idea that flower constancy drives floral differentiation with the more common idea that specialization of flowers for distinct pollinators does so [5, 85–87]. Insofar as these mechanisms occur, they need not be mutually exclusive. Indeed some authors seem to treat them as interchangeable (e.g., [85, 88], which seems largely to stem from confusion in using the term "constancy" to refer to preferences of distinct pollinators for distinct flower phenotypes. When one does distinguish preference from constancy, the mechanisms are in fact seen to differ. Divergence driven by advantages of constancy does not require any plant species to necessarily "give up" any pollinators and become specialized, nor that differences in flower morphology or signal be interpreted as adaptations, respectively, to "fit" different pollinators or appeal to their sensory biases. Furthermore, such divergence might occur in sympatry, whereas divergence by pollinator specialization is more likely to require allopatry [89].

Unfortunately, floral divergence due to benefits of constancy is not easy to demonstrate. Picking flowers randomly from your neighbors' garden may produce a richly colorful bouquet, but natural selection within a single community context, as divergence to enhance constancy postulates, is surely not responsible! To find support for the scenario it is critical to test an observed distribution of phenotypes against some biologically realistic null expectation. An example is the study A. Gumbert, J. Kunze, and L.

Chittka (in preparation) of 23 sets of sympatric and simultaneously flowering plants in five habitats of a nature reserve near Berlin (Naturschutzgebiet Lange Dammwiesen). A *color distance distribution* was generated for each set of flower colors by calculating all bee-subjective color distances between all floral color loci in the bee color space [83]. To test whether the flowers differ more strongly in color than would be expected by chance, 1000 random sets of flower colors were generated by randomly selecting as many species from the flowers of different habitats as occurred in each individual habitat. Each set of real flowers was compared with the overall distance distribution from 1000 such random samples. No consistent effects were detected across different habitats: in one community, flowers appeared to be more similar than expected by chance, in three were they less similar, and in one there was no significant difference between random sets and actual flower color distributions. This effect was mostly due to the locally rare species, not the common ones. In addition, we cannot distinguish between the possibility that character displacement has taken place, or that species which have distinct signals were better pre-adapted to colonise a novel habitat, so that floral diversity in each habitat has arisen by ecological sorting.

The latter finding should not be taken to mean, however, that the hypothesis of adaptive floral color diversity can be rejected even for the common species, or for the habitats where no divergence was found. There are several complications which make such a rejection problematic. For example, not all plants may benefit from having distinct signals. Flowers with low rewards, particularly if they are rare, may receive only very few visits if they are distinct from all others in a community. In such species, convergence on other species may be advantageous [6, 20, 21, 90]. This example illustrates a more general dilemma: the simple null expectation that selection tends to fill “color space” (or some other “phenotype space”) evenly may be wholly in error, and it is not immediately apparent which alternative null expectation is more realistic (this problem bedevils the entire debate over null models in community ecology). Another problem is that some flower species in a community may be unable to change signal or morphology in given directions regardless of selection, because of phylogenetic constraints [83]. Some flowers may be merely transient components of a community, which adds “noise” to any model calculation such as the one described above [6]. Finally, even if there are fitness costs of inconstancy, plants may adapt to minimize the costs themselves, rather than adapting to discourage pollinators from switching. In one study on hummingbirds visiting a set of forest-understory plant species, the birds showed little tendency to be constant, which was consonant with the long travel times between flowers in this environment. Mixed species pollen loads were common on stigmas, but foreign pollen caused little if any reduction in seed set. These plants seemed to have adapted to minimize the cost of having inconstant pollinators [91]. In other cases, sympatric plant species which share inconstant pollinators may place pollen in various body parts of their visitors [92].

In future tests it may be worthwhile to broaden the focus to include studies of single plant species. For example, one might compare floral traits of species which reliably co-occur with other species in some habitats, but bloom singly in other habitats, to determine whether their colors respond to pressures from plants competing for pollinator services [93]. Analyses of flower color divergence in a phylogenetic context would likewise be useful. Because certain morphological features may also favor constancy, one might use morphometric methods to evaluate flowers of species that bloom in different contexts. One might examine species with polymorphisms (either in color or morphology) and evaluate whether the relative frequencies of the morphs differ, depending on the floral traits of potentially competing plant species. An approach different from these is to look for current selection on flowers of species in different ecological contexts, and to determine whether fitness costs of inconstancy are a likely mechanism for any directional selection in the presence of other flowers visited by the same insects. Such experiments are challenging but not impossible [93].

Is Flower Constancy Involved in Speciation of Plants and Maintaining Species Integrity?

The genesis of taxonomic diversity in angiosperms involves both phenotypic differentiation and the development of reproductive isolation. These two processes are often thought to occur in concert, and indeed both processes have been discussed as logical extensions of the microevolutionary processes discussed in the previous section. For example, flower constancy leading to partial reproductive isolation between flowers with different morphologies and signals has sometimes been viewed as a logical step toward the eventual production of sister species that are fully distinct phenotypically and fully isolated reproductively [4, 5, 25, 85]. This is a very attractive scenario, and it joins a parallel scenario in which specialization of flowers for various pollinators (once again presumably in allopatry) drives speciation and maintains sister species as distinct entities once they have arisen (for review and critique see [94].

We have already pointed out the difficulties in determining whether microevolutionary change in flower phenotypes is driven by benefits of constancy. It is even more difficult to evaluate the possibility that macroevolutionary change (species-level phenotypic divergence and reproductive isolation) is so driven. We are forced instead to ponder elements of the scenario in light of model considerations and of the observed strength and expression of flower constancy. Two aspects of the scenario can be considered in turn. First, progress toward speciation in sympatry theoretically requires strong selection, favoring alternative floral phenotypes, coupled with a large initial degree of reproductive isolation, because recombination otherwise would rapidly homogenize any differentiation in phenotypes [95]. The question is therefore whether enough pollinator species are flower constant, whether their constancy is sufficiently complete, and whether the selective benefits of constancy to plants are sufficiently great to drive the process to a conclusion in which stable phenotypic differentiation ensues and reproductive isolation is (at least) nearly complete. Note that, even if all individuals were completely flower constant for life, in the case of social bees, there could still be within-hive transfer of various pollens from bee to bee. In honeybees such transfers are thought to contribute substantially to intervarietal pollen flow in orchards of self-sterile varieties of trees [96].

Second, for sister species to retain both phenotypic distinction and reproductive isolation after primary divergence or secondary contact logically requires equivalent conditions that constancy is great enough to prevent any substantial gene flow, and that its benefits for the plants yield strong ongoing selection on phenotypes.

Although much more work remains to be carried out, what is known of pollinator affinities of plants and of flower constancy suggests that these conditions for sympatric speciation and maintenance of species boundaries are met only rarely. Obligate relationships in which plant species are pollinated by only a single animal species seem to be extremely rare; pollination by a number of species is the common condition [97]. For the scenario to work when plants attract a number of pollinators, it is essential that all pollinators be highly flower constant. However, this is at odds with the observation that many insects are at best weakly constant [6], and that individuals of even “highly constant” species are displaying a flexible behavior that varies with features of flowers and plants (see “Influences of Floral Features on Constancy,” above). Indeed, those few studies that have directly examined pollinator behavior in conditions of sympatry of closely related species report that constancy is far too low by itself to explain any limitation on the production of interspecific hybrids [98–100]. In fact, as in the two species of *Penstemon* discussed above, bees sometimes show not only a lack of constancy but actually a predilection for inconstancy, for example, when the size of one flower species makes it more detectable. Finally, there is the separate question of whether selection on floral features that promote constancy is strong enough to provide the basic motive force in speciation. Both theoretical models and empirical studies indicate a fitness cost of inconstancy [18, 93, 101–103]. For the scenario to work, however, these costs must be large and must not be counterbalanced by fitness costs of sacrificing some fraction of all the pollinators that would otherwise have visited one’s flowers if inconstancy had been maintained [104]. Little is known about these fitness consequences, but it seems to us quite likely that the net fitness benefit to plants simply is not large enough in most cases for speciation to be promoted by flower constancy alone. In summary, we caution against automatic acceptance of this attractive proposition and urge much more focused exploration (including experimental exploration) of its components.

Conclusion

This review does not deliver a single, simple message. This is because there appears to be no single, simple explanation for flower constancy. While we are sure that there are sometimes costs to switching species, and in managing information from visiting several flower species, there is no single general mechanism that sets the constraints. We can assure the reader that insect LTM capacity is not so small as to yield a straightforward explanation for constancy. STM is sensitive to interference during learning of novel stimuli, and possibly limited in capacity. In some studies, bees were reluctant to switch in the first several seconds of flight after a flower visit, even if alternative options were available and familiar. This suggests a temporal constraint of retrieving more remote memories from LTM. Experienced bees, however, sometimes switch very readily between species, particularly if they have recently visited several floral types, and they can therefore apparently juggle the necessary information efficiently. We do not yet fully understand these differences, but one explanation may be that a search along several parameters (such as color and pattern) is more time-consuming than a search along only a single parameter (as in human visual search). The causes of constancy may lie not only in the difficulties of simultaneously accessing all information stored in a pollinator's memory but also in the difficulty of acquiring complete information about the quality of flowers in the outside world. Sampling takes time that might be more efficiently spent in continuing to forage on an – albeit possibly suboptimal – current specialty. Inevitably, sampling new flower species may involve a phase of poor foraging efficiency, which may deter bees from switching. We hope that this review will stimulate further research on all of these possible explanations for constancy, and others not yet envisioned.

It is also important to note that an individual's decision of whether to switch flower species is ecologically nested within a larger scale decision of where to forage. Both bumblebees and honeybees, for example, frequently restrict their feeding to small areas. Animals that choose to feed in monospecific stands are necessarily faithful to a single species, but not for the reasons dicussed here. Some manifestations of constancy are thus epiphenomena of larger scale behaviors. We know very little about habitat selection in general, and almost nothing about how individual insects choose their particular feeding locations. Is the local diversity of flowering species a factor in determining where bees prefer to forage?

The implications of flower constancy for plant evolution are also far from being resolved. To date, there is no good evidence that flowers have evolved to favor constancy, or that constancy contributes to the development of complete or nearly complete reproductive isolation. More careful work is needed here too, in the form of pattern analysis and experimental studies of the fitness costs of inconstancy to plants and of ongoing selection on floral phenotypes in situations with and without these costs. We urge readers to contemplate taking on such studies, which ultimately should contribute to a more exact understanding of the meaning of floral diversity.

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