Flower Constancy, Insect Psychology, and Plant Evolution

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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]

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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 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.