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Artículo de revisión

Floral constancy in bees: a revision of theories and a comparison with other pollinators

Constancia floral en abejas: una revisión de teorías y una comparación con otros polinizadores

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Abstract: Bees make choices about what flowers to visit among the options in the floral market. Bee specialization to visit only one plant species at a time is relevant to maintain the plant-bee mutualism. Angiosperms derive a clear benefit in their sexual reproduction from the fidelity exhibited by the bees; less obvious is why the insects engage in this behavior. The phenomenon of flower constancy in bees is known from more than two millennia ago yet there is no general theory that can explain all kinds of flower constancy. In this paper I review different theories on flower constancy, providing evidence in favor and against each model, and then I discuss the possible scenario in which each behavior can have an ecological advantage. Finally, I present evidence of flower constancy exhibited by other groups of insects and vertebrate pollinators.

Key words: Bees. Floral Fidelity. Memory Limitation. Search Image. Individual Flower Constancy. Energy Maximization. Pollinators.

Resumen: Las abejas hacen escogencias sobre cuales flores visitar entre las opciones disponibles en el mercado floral. La especialización de la abeja en visitar una sola especie de planta al tiempo es relevante para mantener el mutualismo planta-abeja. Las angiospermas derivan un beneficio claro en su reproducción sexual por la fidelidad floral exhibida por las abejas; menos obvio es por qué estos insectos emplean este comportamiento. Aunque el fenómeno de la constancia floral en abejas es conocido desde hace más de dos milenios, sin embargo no hay una teoría general que pueda explicar todos los tipos de constancia floral. En este artículo reviso las diferentes teorías de constancia floral, ofreciendo evidencia en favor y en contra de cada modelo, y de allí discuto el posible escenario en el cual cada comportamiento pueda tener una ventaja ecológica. Finalmente, presento evidencia de la constancia floral exhibida por otros grupos de insectos y vertebrados polinizadores.

Palabras clave: Abejas. Fidelidad floral. Limitación de memoria. Imagen de búsqueda. Constancia floral individual. Maximización energía. Polinizadores.

Floral Constancy in Pollination

Floral constancy is the behavior exhibited by pollinators that restrict visits largely to a single floral type (Waser 1986); this phenomenon has been recognized since Aristotle about 350BC (Grant 1950). Flower fidelity may be guided by innate behavior that evolved through a specialized plant-pollinator relationship. In the fixed constancy all the individuals show preference for the same floral resource and the plant is usually dependent upon the visitor as the pollinator. This type of constancy is distinct from learned fidelity, where different individuals of the same species show preferences for alternative floral resources at the same time and locality (Waser 1986), or where individuals change preferences with experience (Michener 2000; Gumbert 2000). Individual constancy is a particular case of flower fidelity in which individuals of the same species foraging in the same floral patch show different preferences that are irrespective of reward (Wells and Wells 1983, 1986), and seems to be distinct from learned behavior (Çakmak and Wells 1995). Thus, while the phenomenon of flower constancy has been observed for thousands of years, there are now several potential explanations. In this paper I focus on floral constancy as a specialized behavior of short term, exhibited by forager nectivores to cope with particular ecological conditions. I will not discuss the hypotheses concerning with innate floral constancy which is an evolutionary specialization. I also use the terms constancy and fidelity indistinctly so they can be interpreted as synonyms.

The Floral Constancy of Bees

Bees are flower visitors by nature. This is the result of evolution that has led bees to acquire their total source of protein and energy from flowers. Many plants depend on the behavior of bees and have adaptations that ensure the visiting bees become pollinators, and thus facilitate genetic crossing of the plants. Thus, the bee-flower relationship is, in general terms, mutualistic and evidence suggests that this relationship evolved long ago (*ca*. 70 million years) (Crepet *et al*. 1991). However, extreme cases of coevolution and specialization are rare, which indicates the role of bees as a pollinator is not limited by coevolutionary forces. This suggests flaws in the commonly believed hypothesis of coevolutionary specialization. In fact the current views on the plant-pollinator system are controversial because several flower and pollinator traits hint specialization, while the ecological interactions at a local scale are webs that mirror a generalized system (Waser *et al.* 1996, Gómez 2002, Fenster *et al*. 2004, Machado *et al.* 2005).

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The honeybee, *Apis mellifera*, is a generalist pollinator, in part because its colony is "perennial," and the bees have to cope with changes in flowering thorough-and across seasons. The honeybee also has to adapt to changes in flower daily anthesis rhythms, which is a phenomenon that may persuade pollinators to switch flower preference (Endress 1994; Percival 1965), therefore even insects with short life cycles have to face daily changes in food resource availability. Paradoxically, floral constancy is a pervasive behavior in honeybees that is also found in other types of bees and insects, as well as in vertebrate nectivores. Given the variability in the seasonal and daily floral landscapes, it is intriguing why individual bees would show fidelity to any one species of flower. Although flower constancy has been specially studied in honeybees, models have also included other groups of organisms and have posed diverse explanations: cognitive limitations of the pollinator (Lewis 1986; Waser 1986), the formation of a search image by foragers (Heinrich 1975; Goulson 2000), individual constancy due to color context-specific behavior (Wells and Wells 1983, 1986), energy maximization (Stephens and Kress 1986).

Memory limitation

Darwin (1876) realized that the behavior of bees of returning to the same flower type, in effect repeating the same task, allowed bees to visit food sources more quickly than they would if they were alternating between floral types. Darwin suggested that this type of floral constancy can be an adaptation to exploit flowers efficiently. In effect, a memory limited to a particular flower could be an evolutionary advantage since the cost of cognition is reduced while the reward is high. The observations of Darwin also pointed out a limited ability of bees to switch efficiently between different flower types. This difficulty may be interpreted as a limitation to quickly learn about alternative flower types. Under certain scenarios, traveling longer distances between the same target flowers is more costly than handling different types of flowers growing close together. Despite the inefficiency that can be associated with flower constancy, bees remain constant. Waser (1986) and Lewis (1986) proposed that constancy behavior of insects was the result of their cognitive limitations. Cognitive limitations may play a part in determining bee behavior, but it is only one of several factors in operation.

Cognitive limitations of bees have been shown not to exclude their ability to learn to extract food from different flower morphologies. That is to say, the cognition of bees is not so limited that they cannot learn different tasks. Bees, through instrumental conditioning, can learn to appropriately handle a flower to extract a reward. However, the learning process takes several trials, and thus demonstrates a cost of cognition. But, once a bee has learned the morphology of a flower, the handling time is reduced (Heinrich 1979, 1983; Laverty 1980; Laverty and Plowright 1988; Lewis 1986; Keasar *et al*. 1996). Thus, switching between flowers types with different morphologies increases handling time, especially when the floral morphology is complex (Heinrich *et al*. 1977; Lewis 1986; Woodward and Laverty 1992; Chittka and Thomson 1997). Bees exhibit a learning curve, and the cost of learning a new morphology seems to favor constancy to the familiar species.

These observations about flower fidelity and learning in insects suggest cognitive limitations as an explanatory model for bee constancy behavior. The limited memory model (Lewis 1986) predicts that an insect memory for handling a particular flower type will be replaced if new information about a different type of flower is obtained. In other words, when a bee learns about new flowers, she may forget about others. The hypothesis of Lewis explains the observed phenomenon that whenever a bee switches between morphs an increase in handling time will occur. Theoretically, if there were no limitations in a bee memory capacity, once the insects made the initial investment in the phase of learning about alternatives, bees should become less constant and switch between different morphologies without an increase in handling time (Waser 1986).

A separate idea, described as the interference hypothesis, implies that the difficulty to learn, or retrieve, information of several flower species is related to the morphological complexity of the flowers. This hypothesis suggests that bees foraging on floral patches intermixed with floral species of similar morphology should be less constant than if they were foraging in a patch of flowers that are very distinct in morphology (Heinrich 1976a; Laverty 1980). Thus, the interference hypothesis centers on floral morphological differences as a challenge to the bee ability to switch between different flower species. It predicts that the cost of cognition for learning about similar morphologies is lower and so bees should be less constant among similar species.

Bee constancy has limitations–as any given species of flower blooms only during a particular time. Observations show that once a floral resource starts waning, the bee does not continue to look for late blooming flowers of the same type, but readily changes to other resources (Heinrich 1983; Bronstein 1995). The abilities of bees to change between flower species show that they have an evolutionarily encoded mechanism for learning new species when current food sources are failing. This behavior is expected from a generalist pollinator and would not be the result of any sort of co-evolutionary specialization. Both neural and behavioral studies in bees provide clues about the underlying mechanisms involved in the learning of, and transition between, flower species. The studies have uncovered several adaptations that have evolved in bee memory. For example, bees learn fast and can consolidate long term memory (LTM) for particular information associated with food such as color, odor, and shape, but if not reinforced the information will be lost quickly (Menzel 1979, 1985, 1999). Bees must balance between knowledge and relevance; a new food source can be quickly learned if it can be found frequently, but bees will not expend the cost of cognition required to remember the food source if it is infrequently found (Seeley 1985; Menzel 2001). Learning and remembering food sources factors into what is apparently a bee perception of reward as relative rather than absolute (Waddington and Gottlieb 1990). Bee responses to relative rewards translate into a bee ability to perceive its floral resource as waning and to react quickly to this. Thus, flower constancy is impermanent. In bumblebees foragers are prepared to exhibit constancy to exploit food and they are also prepared to exhibit flower infidelity in response to a perception of relative reward decline (Goulson 2003).

A temporally-fixed flower fidelity exhibited by the bee and its corresponding ability to learn new floral morphologies entails certain caloric costs. There are costs incurred in energy loss when bees stay with the target flower species while higher caloric rewards of alternative flowers exist at the same time. There are also costs incurred by traveling in response to the distribution pattern of the plants to which the bee is constant rather than traveling to the nearest reward.

The memory limitation hypothesis suggests that the main benefit the pollinator derives from fidelity to only one plant species, or to several that have similar morphology, is represented in savings in handling times. This parameter can be critical because, unlike other 'predators,' the bees exploit the 'prey' in a pattern consisting of several consecutive flower visits per foraging bout, amounting to hundreds of visits per day. The bees then benefit in what is seemingly a costly system of flower fidelity because even a small difference in handling time will add up in total energy savings. Additionally, bees that stay with the same flower species avoid a cost of cognition in memory formation for new flower types, which is known to be energetically costly.

The functional value of memory limitation can be evaluated in terms of ecological adaptations. Ecological systems may display temporal and spatial homogeneity in the floral landscape that encourages bees to continue exploiting a certain species at a certain time and in a certain place. Some plant species have peak periods of flower blooming (cornucopia in nectar/pollen) that encourage bees to exploit a single floral species (Gentry 1974; Gordon *et al.* 1976). Also, big inflorescences promote fidelity since they present a large reward source that can persist for several days, usually with durations longer than those of individual flowers. Finally, conspecific plants tend to grow together offering an abundant resource that can be efficiently exploit with a limited memory, or if the plants are distributed in heterospecific patches, the plant species will have distinct floral structures, which according to the interference hypothesis also promotes floral constancy. These ecological factors suggest how memory limitation functions within ecosystems to create a rate of reward production sufficient to keep the pollinator enticed.

The memory limitation hypothesis has received support from studies with butterflies, which limit cost of cognition by feeding from a single flower source (Lewis 1986, 1989, 1993). Memory interference models have also been tested in solitary bees and bumblebees; again, memory limitation hypotheses have received support by demonstrating a flower visitation mechanism similar to that found in honeybees (Waser 1983, 1986; Gegear and Laverty 1998). Finally, studies on the adaptability of bees have been conducted that support the memory interference hypothesis. It has been found that bees switch between similar flowers of different species with minimal interference (Laverty and Plowright 1988; Chittka and Thompson 1997; Gegear and Laverty 1998). When they attempt to switch between two complex flowers, bees demonstrate an increased handling time (Gegear and Laverty 1998). Taken together, memory limitation theories seem to predict bee behavior and rationalize flower fidelity. However, these theories still lack the ability to explain some types of flower constancy. For example, the context-dependent individual constancy found in honeybees cannot be explained in terms of the handling costs implied by different flower species (Wells and Wells 1983, 1986; Wells *et al*. 1992). Additionally, memory limitation hypotheses fail to explain bumblebees that can learn to handle two different types of flowers without an increase in handling time every time they switch between types (Chittka and Thompson 1997). Bumblebees have been shown to be able to learn two different colors and two different odors and distinguish them from other flowers. Bumblebees can also learn individual flowers in large arrays, and then visit them systematically (Thompson *et al.* 1987). This evidence suggests that bumblebees form separated memories for the plant species present in the floral patch. Honeybees also seem to exhibit memory capacities that cannot be explained by memory limitation theories. Honeybees form multiple memories about flowers differing in the rate of nectar production (Greggers and Menzel 1993; Greggers and Mauelshagen 1997). Honeybees also seem to develop multiple memories about flowers that present rewards at different times of day (Koltermann 1974; Gould 1987, 1991). Studies that demonstrate the honeybee ability to create multiple memories about food resources conflict with the memory limitation hypotheses that suggest bees cannot store information about more than one flower species. Thus flower constancy in bees cannot be explained by memory limitations: bees exhibit the ability to learn and recall information about multiple food resources. Other hypotheses emerge to help explain flower fidelity based on certain visual cues including a "search image" hypothesis.

Search image

It has been proposed that insects exhibit floral constancy because they use specific search images to find their targets (Heinrich 1975; Goulson 2000). The search image concept is related with what is known in psychology as selective attention. Selective attention is particularly useful for predators learning to detect cryptic prey. A search image allows a predator to pay attention only to particular visual features of the prey that best distinguish them from the background. There is evidence that both honeybees and bumblebees can use selective attention when distinguishing between floral types (Klosterhalfen *et al*. 1978; Dukas and Waser 1994). It is known that the bee brain has a limited capacity to process information simultaneously (*i.e*., bees have narrowly focused, limited attention). In honeybees it has been shown that short term memory (STM) is vulnerable to extinction if there is no reinforcement to consolidate the information in a lasting form of storage (Menzel 1979, 1985; Chittka *et al*. 1999).

The search image theory proposed by Tinbergen (1960) suggests that predators have selective attention and thus focus on a particular prey. Goulson (2003) refined the search image hypothesis by associating it with the idea of predators looking for cryptic prey. Dukas and Ellner (1993), using the search image hypothesis, made the prediction that if predators (pollinators) have a limited attention and if prey (flowers) are cryptic, then predators should focus all their attention on a single prey species, but if prey are conspicuous, then pollinators would divide their time among types (Goulson 2003). There is some evidence that flowers may be cryptic for pollinators (Endler 1981; Goulson 2003) and the color contrast between flowers and the background in which the flowers are located has been recognized as part of the signal perceived by the pollinators (Chittka & Kevan 2005). These studies suggest that cognitive factors involved in finding flower sources in a constantly changing environment can be nearly analogous to lions searching for camouflaged prey in their territories.

The concept of a search image is appealing: taking the size of a bee into account, compared with the landscape scale in which flowers are distributed, perhaps flowers are for bees, in effect, an elusive and hidden prey. Bees need signals to locate flowers, and they will respond positively to strong signals such as a flower's size and color. That bigger signals attract bees implies that flowering plants have selective pressure to signal in order to receive pollination services. There are several ways in which plants can respond to the requirement to signal pollinator species such as the honeybee. They may exhibit big flowers: this scenario may be costly for the plant to maintain large flowers producing reward for a period longer enough to get fertilization of its ovules, and also risky in case of pollination failure, so this evolutionary strategy of solitary flowers has not prospered in Angiosperms. Alternatively, these plants have evolved inflorescences to present rewards in several discrete and smaller units (flowers), allowing them to dispense rewards regulated through the time. The increase in number of flowers per reproductive shoot balances the risk of sexual reproduction failure for individual plants.

Another technique to attract pollinators is for flowers to differentiate themselves from the surrounding foliage: flower color that contrasts with the bracts and foliage may trigger pollinator response. Plants may also retain corollas of pollinated flowers to maintain a larger signal to pollinators. Pollinators may be attracted by growing patterns that plants adopt: either growing clumped with conspecifics, or growing clumped with heterospecific plants that have the same floral color signal. The visual signal of flowers has important consequences for both the pollinators and the plants: visual cues are a probable mechanism involved in floral visitation patterns. These visual cues may explain floral constancy under certain scenarios (*e.g.* blooming peaks in which conspecifics are abundant). The search image theory has some limitations to explain bee flower fidelity: if the search image is formed for a particular flower trait (*e.g.* color) that type of search image would promote floral inconstancy in floral landscapes having different species with the same flower color. However, it has been observed that bees still exhibit flower constancy in floral landscapes of similar-colored flower species.

Some evidence suggests, however, that plants have adapted to take advantage of the search image of pollinators. The use of a color search image may benefit plant species sharing pollination services in a way that reduces plant competition for limited pollinators (Feinsinger 1978). This apparent manipulation of the pollinator color constancy creates potential costs for the foragers. Pollinators exhibiting color constancy may incur a cost by visiting similarly colored flowers of several species and being rewarded inconsistently by both the amount and the quality of the nectar produced by different flower species. Additionally, color constancy may have the added cost of increased handling times associated with different floral morphologies in plants with the same flower color. Given these potential costs, color constancy as a result of search image memory seems to be a somewhat inefficient foraging strategy.

On the other hand, the cognitive mechanism underlying search image is not well understood. The search image phenomenon could be an economic form of memory based on elemental conditioning to a single stimulus. This mechanism could function by saving costs associated with storing information. But, any savings would be short term because the utility of any information is restricted to a short period. For pollinators, such as bumblebees that follow a trap-line strategy of flower exploitation, a search image mechanism would be completely inadequate because bees need to switch between flowers of different structure and color as they move along the trap-line. It is interesting that "bumblebees fly slowly between flowers and between plants." (Pyke 1979). This observation may indicate that bumblebees have a different searching strategy and invest more time in order to discriminate between different types of flowers than do honeybees. Bumblebees may, in this way, depend less on a color search image.

While the exact cognitive construction of search imaging is not fully understood, and there are undeniable costs associated with this foraging strategy, search image memory demonstrates some aspects of streamlining the process of gathering food. Search image memory increases the speed at which a bee may detect a flower type that has previously provided a reward. Foraging following a search image may create an easier decision making process upon an encounter with the "expected" signals. The converse, of course, is that reaction times may be longer when subjects do not have a prior expectation of what are they looking for. Chittka *et al.* (1999) found that bees flying may encounter a new flower every 0.14 second. It seems unlikely that in such a short time the bee would retrieve the information or memories necessary to recognize a flower, recall the motor skills required to handle the flower, and make the economic decision whether to visit it or not (Goulson 2003). Rather than process many variables in a decision-making procedure, it seems plausible to use a simple visual signal and run the risk of some mistakes.

The search image hypothesis does predict floral constancy in many cases. Temporal and spatial homogeneity in the floral landscape would allow search image memory to benefit pollinators. Search image memory would also recall large inflorescences, conspecific plants growing together, and heterospecific with similar flower color, reward composition, and morphologies; in this latter case, however, the more rewarding flower type has to also be the most abundant flower type. Several studies have demonstrated the viability of the search image hypothesis. Many researchers have observed that pollinators switch between plant species that have similar flower color (Waser 1986; Kunin 1993; Laverty 1994; Chittka *et al.* 1997; Gegear and Laverty 2004), and that the production of hybrid seed fails among flower color varieties of the same species (Grant 1949, 1950; Free and Williams 1973, 1983).

This said, studies have also suggested flaws in the search image hypothesis. Bumblebees utilize flowers of different species in densities proportional to their nectar rewards and unrelated to their colors (Heinrich 1976b; Pleasants 1981). Among honeybees, color is not always the key factor in flower constancy (Greggers and Menzel 1993). Therefore, search image may not be the primary cognitive mechanism that bees use in foraging.

Individual constancy

Individual constancy describes the fidelity exhibited by the honeybee to a flower of a single color irrespective of the reward (Wells and Wells 1983, 1986; Hill *et al.* 1997). This type of constancy is innate (Çakmak and Wells 1995) and not labile; it is not susceptible to modification with experience because the bee does not sample between alternative resources. It is important to note that in experiments concerning individual constancy, the observed fidelity to one color by an individual is not the result of lacking a choice. Further, floral preference cannot be associated with innate preferences of the species because different members of the same population, or even of the same colony, specialize on different flower colors (Wells and Wells 1983, 1986; Hill *et al.* 1997). Individual fidelity exists even under conditions where alternative flower colors offer different caloric rewards. In the experiments of Wells and Wells (1983), the two alternative colors were made distinct in reward quality (0.75 M vs. 2 M) or volume (2 vs. 20 µl). Even these significant differences failed to elicit a behavior of optimal choice.

Individual constancy is similar to the search image model with an adjustment made to the definition provided by Lawrence and Allen (1983), where the predator learns to see the cryptic prey after a chance encounter and selectively uses those cues that allow it to distinguish the prey from the environment. It is as if the "search image" is formed in only one trial, or first choice, and after that the alternative color is left in the background. The bee becomes unaware of the other flower colors. The limitation to seeing the alternative color may be caused by a physiological restriction imposed by the activation of mutually exclusive nervous wiring associated with each color. Hill *et al.* (1997) suggested that the distance between two flower colors in the bee visual representation (perception of color: Chittka 1992) may have an effect on the dual behavior observed in honeybees when foraging on bicolor patches. That is, on patches made of blue and white flowers the bees use both colors of flowers randomly whenever the reward is the same in both color morphs. However, as soon as one of those colors becomes more rewarding, the bees show preference for that flower color and behave in accordance with energy maximization theory. However, bees foraging on patches made of flower colors distinctive in the bee color space, such as blue and yellow, show individual constancy to the color chosen in the first visit (but see Waddington and Holden 1979; Marden and Waddington 1981). This behavior has been consistently observed in different experimental designs (Wells and Wells 1983, 1984, 1986; Hill *et al*. 1997, 2001; Çakmak and Wells 1995; Sanderson *et al*. 2006). This type of floral constancy is resistant to experience, and, because it conflicts with theories of optimization and efficiency, it is rather puzzling. It seems to be that the establishment of individual constancy occurs if the bee makes a choice while flying. The hypothesis that individual constancy occurs when bees are flying explains behavioral differences when the flowers offered are pedicellate (Wells and Wells 1984), but not when the flowers are sessile where the bees can walk from flower to flower (Waddington and Holden 1979). Noting that individual constancy seems to come from the quick decision making process while flying between flowers, individual constancy may be related to a type of search image, a useful mechanism to make quicker decisions while bees are flying.

Search image may have a genetic component involved, associated with either the visual field sensitivity of bee species, or with other adaptive features that help an individual respond to environmental pressures such as predation. There is evidence that subspecies of *Apis mellifera* exposed to high levels of predation present less pronounced individual constancy (Çakmak and Wells 2001). The genetic variation may be expressed not only at the subspecies level, but also at the colony level. In individuals of *Apis mellifera ligustica,* which were forced to visit a patch of flowers of only the alternative color, individual constancy reappeared to the original flower color once the choice was restored (Hill *et al*. 1997). The ease with which individuals "see" one of the two colors and the preference shown to that color may indicate a genetic component is involved in this behavior.

The genetic encoding of a search image that is not necessarily efficient incurs costs on the species. Once a search image is developed, the bee passes flowers of some different colors that may be more rewarding than the target flower type. Bees can make "mistakes" and hit different flower species of the same color. Together, these costs associated with search image-decrease the average reward harvested during the foraging trip, either because it implies a costly handling technique or because the reward offered by the "mimetic color" is lower than the targeted color.

Evolution rarely selects for inefficiency, so search image-based constancy must demonstrate some advantages. A search image may help bees increase detection of a flower type that has provided an "adequate" reward, maybe over an internal threshold, in the past**.** It is also possible that a search image increases harvest efficiency when the dominant flower type in the floral landscape corresponds to the targeted type. Individual constancy may also attenuate intraspecific competition in food exploitation, since members of the same species, and of the same colony differ in the flower color chosen to visit.

Floral constancy occurs most frequently when a mixed array of flowers made of very different colors in the visual map of bees is encountered by a forager. These flowers, spread dichotomously across the visual spectrum of the bees, support the search image hypothesis. The individual constancy hypothesis has been supported in observations of bees foraging on dimorphic patches of blue and white or blue and yellow flowers, and on tricolor patches: blue, white and yellow (Wells and Wells 1983, 1986; Hill *et al.* 1997, 2001; Sanderson *et al.* 2006). Spontaneous color choice in the honeybee depends on the wavelengths of the alternative colors (Menzel *et al.* 1974). Observations of honeybees in a natural situation are consistent with the results obtained using artificial flower patches. Observations of honeybees visiting *Lantana camara* L. which has purple and yellow flowers show that individual bees in consecutive visits moved between flowers of the same color, even though the alternative color was present in the same inflorescence.

Some studies on the foraging ecology of the honeybee using yellow and blue flowers have not reported individual constancy (Waddington and Holden 1979; Marden and Waddington 1981). However, this finding does not necessarily refute the individual constancy hypothesis (Wells and Wells 1983, 1986) because the flower patch used in those studies has a structure that is an "inflorescence" like that where bees can walk between 'florets' in consecutive visits. The design of the Wells' patch is called a "population" type (Wells and Wells 1984) in which the bees alight on the flowers and have to fly between consecutive visits. Opfinger realized in 1931 that bees learn color only when they approach the flower (Menzel and Erber 1978). It is possible that bees walking between flowers guide their search by cues other than vision. Instead, walking bees may be attuned to stimuli such as the aromas or the texture of the flowers. The flower patch structure affects the flower choice of the honeybees. Bees foraging on flower patches of the population-type exhibit individual constancy, while those that forage on patches of the inflorescence type do not (Wells and Wells 1984). Thus, search image may be a technique honeybees use to maximize energy by making color-based decisions while in flight. Without the energy expenditure of flight, bees can use other resources to sample flower targets.

Energy maximization

Pollinators have strict energetic requirements that presumably make them quite selective in their floral visits. They should choose those flowers that best meet their energetic needs (Real 1981). Optimal foraging theory makes the assumption that natural selection will favor foragers that are able to attain maximal net energy intake (Pyke *et al.* 1977; Stephens and Krebs 1986). However, other factors such as nutrient requirements, risk-sensitivity to predation or starvation, mate searching, nest provisioning, and floral landscape features may cause the observed foraging behavior of a pollinator to differ from the predictions of energy maximization. Natural selection acts on the honeybee at the colony level, however colonies of the same species compete among them for the floral resources available at a time. Thus, the differential success of the colonies to harvest and store food efficiently in order to overcome winter and reproduce, depends on the skills of their individual forager bees. Both nature and nurture affect foraging quality, and the fitness of colonies that have skilled foragers will be greater than the fitness of colonies less competitive in the process of harvesting food. Therefore the optimal foraging theory assumption about the relationship between fitness and the efficiency in food exploitation still applies to the social honey bee.

Pollinators have to make economic choices about what floral patch to visit, what type of flowers to visit in a sequence, and how far from the nest to search for flowers. Other factors involved in the energetic profit resulting from a floral decision include the forager experience manipulating a floral type and so its perception of handling time, the social organization and the labor division. Additionally, foraging for nectar and pollen may have different consequences on load sizes, handling times, and traveling distances, given that nectar is the bee basic fuel. As a consequence of these multidimensional situations, it is impossible to predict only one optimal situation. Even by restricting the situation in which the currency to maximize is only caloric intake, the optimal value will still be dependent on the conditions of the floral landscape. For this reason, it is practical to view costs and benefits of foraging behavior as explicit tradeoffs.

An economic choice is based on an informed decision, and most decisions involve some sort of tradeoff. Economic choice implies that the bee's decision is based on information learned as a result of some kind of sampling. Learning, either as a result of an active sampling process (assessing media and variance) or as a passive mechanism of association, requires the ability to discriminate among alternative flower types. The number of sampled flowers required to assess alternative rewards and these may be extremely large depending on the variance in those rewards. Intrinsic variance in the production of nectar, as well as that caused by the presence of other floral visitors, can make the evaluation process very expensive. Search image formation after only three flowers visited of a species providing food would interfere with the intended sampling process. This three-visit base decision will "trap" the organism and force it to focus attention on capturing as many acceptable target preys as possible in a minimal time. In this case, the search image strategy, or the strategy of "pure patch exploitation" (no sampling), would be optimal for maximizing energy intake because it saves handling time between conspecifics. Energy maximization using search image recall depends on the structure of the floral landscape in which the interaction occurs.

Floral morphology affects flower choices of pollinators and the fidelity exhibited by those to a particular flower species. Different flower species require different handling techniques which, in turn, affect the economy of floral decisions. Individuals of generalist species forage as specialists to increase the rate of energy intake by staying constant to a flower species that requires the same handling technique (Heinrich 1976a). But this constancy is not fatally rigid. Individuals of even highly constant species may show flexibility or inconstancy under the influence of floral morphology (Chittka *et al*. 1999). Similar morphologies of different species may require the same handling technique, which allows the pollinator to switch among morphs without increasing handling time. Neither color nor handling time by itself explains fidelity because net energy returns can be distinct for flowers with the same handling mechanism. Flowers may offer the same reward but require different handling times, and in this latter case the bees prefer the color morph with lower handling time (Waddington and Gottlieb 1990; Sanderson *et al*. 2006). Bees facing the tradeoff between handling time and reward will behave as optimal foragers; they maximize energy intake choosing either the floral type with higher reward (Heinrich 1976b, 1979; Wells *et al*. 1992), or the floral type with shorter handling time (Laverty and Plowright 1988). Within ecosystems, the decision to visit a target flower rarely involves only the variable of handling time versus reward.

Bees must travel from their hives to acquire nectar. Both the traveling time and the quality of the nectar become important factors in the economic decisions of the bees. The effects of the spatial arrangement of flowers on constancy are predicted when there are no handling time costs in switching (Chittka *et al.* 1999). If flowers of the same type are sparsely distributed, the probability of not encountering the same target type increases, so the costs of longer searching may surpass the potential costs of switching flower type. In cases of sparsely distributed targets, bumblebees are more prone to infidelity (Chittka *et al*. 1999). Studies with artificial flower patches in which two color morphs were presented with the same reward have shown that bees maximize energy intake by visiting the closest flower color in a blue-white patch, but they maintain individual constancy in a blue-yellow patch and travel longer distances between morphs of the same type (Hill *et al.* 2001). It seems that early formation of a search image impedes the bee perception to "see" the alternative color, and that restriction impedes energy maximization. The response of the bee to energy maximization is context dependent. Marden and Waddington (1981) found that honeybees foraging in artificial flower patches respond to traveling distance, usually choosing the closest flower species regardless of color. The discrepancy between these results and those of Hill *et al*. (2001) can be caused by context dependent factors of the floral patch affecting the foraging response of the bee (as was discussed before). Solitary bees have also shown to be able to asses the quality of alternative flower colors, learning and developing flower constancy for the flower color that returns a higher net energy (Amaya-Márquez *et al*. 2008). A formula for determining energy maximization in relation to flower constancy ultimately seems to break down among the many context variables. But, flower constancy is not a behavior found in bees alone, which suggests that there is some definite evolutionary advantage to this behavior.

Floral Constancy of Other Insects: Beetles, Flies and Butterflies

Flower constancy was a behavior initially observed in bees (Waser 1986). However, it has also been reported for butterflies (Lewis 1986) and other types of insect pollinators, including beetles and flies (Weiss 2001).

Pollination by beetles is more common in the tropics than in temperate regions; palms and plants of the family Araceae present specialized mechanisms of thermoregulation in their inflorescences to disperse aromas attracting beetles (Proctor *et al.* 1996; Bernal and Ervik 1996; Nuñez-Avellaneda and Rojas-Robles 2008). There are also several plants of the Asteraceae family that are visited by beetles in temperate habitats. Beetles visit the flowers in response to sensorial attraction to odor, especially aromas emitted by the inflorescences (Young 1986; Eriksson 1994). Beetles are attracted by odor at long distances and use color as a close range cue (Pellmyr and Patt 1986). Floral constancy has been reported in beetles (De Los Mozos Pascual and Domingo 1991; Englund 1993; Listabarth 1996). Although it is known that beetles can recognize and distinguish colors, it is not known whether flower fidelity in beetles is innate or learned (Dafni *et al*. 1990). There are many studies on the cognitive abilities of pollinator beetles that infer the effect of learning and memory in floral choice, but most are inconclusive (Weiss 2001).

As is the case of beetles, little is known about the mechanisms that contribute to flower fidelity in flies. Flies of the family Bombyliidae and Syrphidae exploit flowers as a source of food. They have specialized mouth parts to extract nectar, but they also chew pollen (Faegri and van der Pijl 1979). The importance of flies as pollinators has been acknowledged (Larson *et al*. 2001), and there seems to be flower constancy in this group of insects. Flies can perceive color and odor, and they use those cues to locate rewards in the flowers (Hernández de Salomon and Spatz 1983; Troje 1993). There is evidence that supports the ability of flies to associate color with reward (Fukushi 1989). Furthermore, they can be conditioned to odor (Fukushi 1973; Spatz and Reichert 1974; Prokopy *et al*. 1982). Although flower constancy in flies has been reported (Goulson and Wright 1998), more studies are needed to determine the factors of their floral fidelity.

Butterflies are a somewhat better understood pollinator than are flies and beetles. Floral constancy in butterflies has been reported (Lewis 1986), and this behavior has been explained through a hypothesis of limited memory similar to the hypothesis suggested for bees (Waser 1986; Goulson *et al*. 1997). There is evidence that both butterflies and moths can rapidly associate color with food (Swihart 1971; Swihart and Swihart 1970; Weiss 1995, 1997; Kelber 1996). They also exhibit an ability to learn handling techniques to manipulate flowers (Lewis 1986; Kandori and Ohsaki 1996; Cunningham *et al*. 2003). Butterflies have good spatial memory (Kelber and Pfaff 1997) that plays a role in relocating places and flowers that have previously provided a reward, or to reach a roosting place (Waller and Gilbert 1982; Kelber and Pfaff 1997). Flower choice in butterflies may even be guided by a color search image, again similar to bees. Butterfly search image may also be exploited by deceptive plants whose flowers are the same color as the model producer, but producing no reward (Johnson 1994). Unlike bees, butterflies use nectar as a source of amino acids. Perhaps this use of nectar for protein provides a rationale for flower constancy. Butterflies may respond to an expected amino acid composition, and this expected amino acid composition may explain the floral constancy exhibited by these insects (Gardener and Gillman 2002; Mevi-Schutz *et al*. 2003). Floral constancy is also found among certain vertebrate species - again suggesting that, despite certain costs, the evolutionary advantages of floral constancy tends to benefit the individuals that exhibit such behavior.

Floral Constancy in Vertebrate Pollinators

Initially, it would seem that nothing could be more different than birds and bees. Many vertebrates live for several years - in the case of hummingbirds around 4-5 years. On the other hand, insects have short life-span cycles. Organisms with long life cycles are exposed to greater ecological heterogeneity, making food specialization unlikely. For those organisms the value of cognition is probably increased for learning and predicting phenological processes occurring in larger spatial and temporal scales. Vertebrate pollinators may use long-term memory to exploit the phenological cycles of flowering plants at a regional level. According to Bronstein (1995) pollination from vertebrates is more common in the tropics than in temperate ecosystems. Bats and hummingbirds are prime examples of vertebrate pollinators.

Hummingbirds, like bees, demonstrate a form of floral constancy. Hummingbirds defend good floral patches against competitors. The birds, in effect, engage in an obligate floral constancy since they do not move from the tree or the floral patch being defended. It has been proposed that hummingbirds are generalists; they use the flower species in a floral patch in proportion to their abundance (Kodric-Brown and Brown 1978), or they trap line (Gill 1988). Trap lining is a form of solitary foraging that can ameliorate competition for food that is socially exploited. This foraging strategy is exhibited throughout the taxa of nectivore pollinators. Trap lining has been reported in bumblebees and in euglossine bees (Janzen 1971; Heinrich 1979), hummingbirds (Gill 1988), bats (Frankie and Baker 1974; Heithaus *et al*. 1975; Fleming 1992), and butterflies (Gilbert 1975). Thus, organisms with good spatial memory will benefit from this cognitive ability to track changes in resources. It is not well known whether trap line foraging bouts are marked by floral constancy or by visitation to different flower species in the route. However, analysis of pollen loads have shown that individuals of generalist species of hummingbirds, both hermits and non-hermits, carry on average only 2 or 3 different types of pollen grains (Amaya-Márquez 1991; Amaya-Márquez *et al*. 2001). These results suggest that hummingbird species, in spite of being generalists, exhibit individual floral constancy, at least temporally. The efficiency in food intake by specializing in one flower species was given by Darwin (1876) to explain the floral fidelity of the honeybee; however, the same reason can be used to explain this behavior in hummingbirds.

There is evidence that flower choice in hummingbirds is based on energetic considerations, which is consistent with the energy maximization model. The birds are able to assess nectar quality/quantity (Stiles 1976; George 1980; Meléndez-Ackerman *et al*. 1997), and they choose flowers that maximize energy intake (Bolten and Feinsinger 1978). However, other factors also affect floral choice. Sometimes hummingbirds generalize color across flowers (Healy and Hurley 1998). In this case, color choice is not based on energetic considerations. In the same vein, flower choice based on a previous learned association, rather than on the handling time imposed by morphology, has been shown in experiments that modify color patterns of the same morphology (Hurley and Healey 1996); however, at other times the birds are able to discriminate within and between plant species. Learning theories probably can account for the factors leading to these different behaviors. It will be of interest to know the functional value of the excluding criteria the birds use to make a flower choice. At the moment, it is known that learning plays a role in flower exploitation by hummingbirds as it does in bees.

Hummingbirds, like bees, are not born with innate search images to exploit particular flower species, but rather they learn to associate color and reward. In spite of exhibited preferences for red flowers and the contrast this color produces with the green foliage (Stiles 1981) and for other flower color combinations naturally found in flowers of tropical plant species pollinated by these nectivore birds (Amaya-Márquez *et al*. 2001), hummingbirds learn and use information about color in flower choice (Bené 1941, 1945; Goldsmith and Goldsmith 1979; Gass and Sutherland 1985), patterns (Healy and Hurley 1995), and location of the flowers (Hurley and Healy 1996; Bené 1941). Hummingbirds can be trained to color; they can remember specific locations where they have found food (Miller and Miller 1971; Gass and Southerland 1985). The birds use the information hierarchically: first, they use spatial memory to arrive at the location, and then they use information for flower cues (Healy and Hurley 2001). Hummingbirds return to the precise places where feeders have been located previously, even if the feeders have been removed. Good spatial memory is required to avoid re-visitation to flowers before they have replenished nectar. Also trap liner foragers need to have excellent memory to relocate plants in a foraging route. In fact, long term memory has been shown in birds visiting places before the plants start blooming. It may be expected from a vertebrate with a long life-span cycle, facing temporal heterogeneity and using phenological times, that it will revisit good flower patches. Species of hummingbirds make altitudinal and latitudinal migrations following seasonal weather. In contrast, it has been reported that hummingbirds have a limited memory to remember spatial positions at the scale of individual flowers (Miller *et al*. 1985). Obligate flower constancy in hummingbirds has also been reported when there are no choices in the floral landscape: the birds visit the only flower species available at a time (Waser 1979).

Like hummingbirds, beetles, and flies, pollination by bats is a phenomenon more common in the tropics than in temperate areas (Bronstein 1995). Nectivore bats are generalists, but, like hummingbirds, they can exhibit obligate flower constancy temporally when there are no other resources available (Waser 1979) or when particular plant species (usually trees) make an abundant offering by peaking nectar production as a consequence of several individual plants blooming simultaneously. Unlike hummingbirds that are solitary species and forage solitarily, bats form roosting places that work as information centers like the hive does for bees. Odor cues obtained from successful foragers are used by other bats, and thus social information can affect flower choice in these mammals. However, social foraging generates pressure for food resources, except when they are abundant. As this is not always the case, bats of the New World (Microchiroptera) have developed an alternative strategy. The use of sonar and echolocation has allowed them to adopt trap line behavior (Frankie and Baker 1974), which implies the use of a foraging strategy based on individual experience.

Birds, bats, and bees have a surprising number of overlapping qualities as pollinators. Vertebrate and invertebrate pollinators, in spite of great differences in life cycles and brain complexity, exhibit similar strategies to exploit floral resources in a floral landscape marked with high environmental heterogeneity. Pollinators are usually generalists, feeding from flower species changing in spatial and temporal dimensions. However, individual patterns of foraging are characterized by specialization on the resource returning the highest rates of energy intake to the forager. This behavior is consistent with the predictions of optimal foraging theory (Pyke 1978; Stephens and Krebs 1986) and can represent one form of a more generalized way animals exploit food resources (see West-Eberhard 2003 for a review). However, other factors affecting fitness, joined to the specific nature of food exploitation determined by each species genetic heritage, lead to a diversity of foraging behaviors that reflect particular trade-offs. In spite of the temporal specialization in food, pollinators can change flower species. Hummingbirds, bats, and butterflies embark in latitudinal or altitudinal migrations in response to temporal and local changes in resource availability. Therefore, temporal flower constancy changes occur both in vertebrates and in invertebrate nectivores. However, the short life span of insects might lead them to life-time specialization for only one food resource. Bronstein (1995) has pointed out that vertebrate pollinators have to assess floral resources at a broad spatial scale. Vertebrates and invertebrates learn about food quality, and they develop long-term memory for places and flowers. Mass blooming plants, especially tropical trees, allow vertebrates to exploit food socially. However, this feeding strategy is dependent on the cornucopia duration of floral resources; thus nectivore foragers have adopted alternative strategies of food exploitation, such as trap lines.

Across taxa, nectarivore pollinators display many similar behaviors. Most notable among these behaviors is flower constancy. Even so, the flower fidelity of pollinators appears to occur for many different reasons, both within taxa and among widely divergent taxa.

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