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THE FLOWER FIDELITY OF THE HONEYBEE

Balarısı Çiçek Bağımlılığı

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> "*On any one flight the bee does not go about to flowers which are different in type*: [rather, she travels] *for example from violet to violet, and does not touch any other to that point where she flies in to the hive*" (Aristotle 330 B.C.).

Abstract: Since the time of Aristotle, it has been observed that honeybees show remarkable fidelity to a plant species when visiting a patch of flowers to forage. This pollinator flower constancy, in fact, is not limited to a few flowers in a set of sequentially visited flowers. A mere 6% of the pollen in a pollen-load returned to the hive by a forger is from more than one plant species (*e.g.* Free 1963; Moezel *et al.* 1987). In the agricultural literature this flower fidelity of honeybee foragers became known as '***crop attachment***'. Here, we review what is known about why a honeybee typically chooses to forage from a single flower type despite the wide range of options available to it. Although the flower fidelity of honeybees is legendary (Aristotle 330 B.C.; Virgil 30 B.C.; Butler 1609; Benett 1883; Maeterlink 1901; Ribbands 1953; Hill *et al.* 1997), flower constancy at times is not observed, and this is important when considering why flower fidelity is so prevalent among honeybee foragers.

Keywords: Honeybees, flower fidelity, foraging, models

Özet: Aristo zamanından beri arıların çiçekleri ziyaret ederken belli bir bitki türüne gösterdiği bağımlılık bilinmektedir. Aslında bu çiçek bağımlılığı peş peşe ziyaret edilen çiçek grupları arasında birkaç çiçek ile sınırlı değildir. Polen yükü ile kovana dönen yayılmacı arının getirdiği polen yükünün ancak %6'sı birden fazla bitki türünden toplanmıştır (Ör. Free 1963; Moezel *et al.* 1987). Tarım literatüründe arıların çiçek bağımlılığı "***ürün tutkusu"*** veya ilişikliği olarak geçer. Biz burada balarılarının bilinen çevrede birçok çiçek varken tek tip çiçeği neden seçtiğini açıklamaya çalışıyoruz. Gerçi arıların çiçek bağımlılığı efsane gibi bilinmesine rağmen (Aristotle 330 B.C.; Virgil 30 B.C.; Butler 1609; Benett 1883; Maeterlink 1901; Ribbands 1953; Hill *et al.* 1997) bazen bu çiçek bağımlılığı görülmez. Bu, balarılarında çiçek bağımlılığının neden yaygın şekilde olduğu düşünüldüğü zaman önemlidir.

Anahtar kelimeler: Balarıları, çiçek bağımlılığı, yayılma, modeller

I. Fidelity from a Lack of Choice?

The simplest explanation offered for the flower fidelity of honeybees is that they generally do not experience a choice of flower types at a specific locality, and thus if a choice existed honeybee fidelity would be less consistent. Several lines of research, however, have dispelled this myth.

First, agricultural experiments attempting to produce hybrid seed in crops as diverse as kale, Brussels sprout, beans and alfalfa have failed due to the behavior of honeybee foragers (*e.g.* Boren *et al.* 1962; Hanson *et al.* 1964; Faulkner 1971, 1974; Free & Williams 1973, 1983; Currie *et al.* 1990). In these experiments, different varieties of a particular crop species were intermixed in an attempt to produce hybrid seed. Yet, even the most determined of these experiments, in which a large number of foragers were caged with equal numbers of two alfalfa clones, resulted in less than 5% hybrid seed –even though 50% was expected and both alfalfa varieties had heavy seed set (Hansen *et al.* 1964).

Second, honeybee-forager flower-fidelity is mirrored in experiments with artificial flower patches as exemplified when presenting bees yellow and blue flower choices in close proximity (*e.g*. Wells & Wells 1983, 1986; Cakmak & Wells 1996). Here, rewards, number of foragers, *etc*. have been eliminated as the root for flower constancy. In this situation, flower fidelity does not diminish, but has a rather peculiar characteristic, which will be explained in detail later.

Finally, observations of bees in complex habitats where floral choices exist show the same flower fidelity exhibited by foragers as that observed in agriculture and artificial flower patch experiments (*e.g.* Clements & Long 1923; Heinrich 1993; Johansen & Mayer 1987; Moezel *et al.* 1987). For example, although the shrub-lands of the northern sand-plains of western Australia are floristically diverse, pollen collections by bees are not (Moezel *et al.* 1987). Similarly, when watching individual bees forage in mixed flower gardens, each bee observed exhibits extreme flower-type fidelity (Clements & Long 1923). Most habitats consist of several to many patches of flowers, some without floral diversity, but many with different flowers to choose among, and thus pollinators typically have foraging choices to make (Menzel 2001). Hence, we are well aware that flower constancy behavior is not simply a consequence of a lack of alternative resources- although when floral diversity is absent, of course, flower fidelity occurs.

II. Forager Memory Limitations?

The flower fidelity of foragers is not unique to honeybees, although primarily described in them. Bumblebees (*e.g*. Heinrich *et al.* 1977), butterflies *(e.g.* Lewis 1986), solitary bees (Gross 1992), and even dipterans (Goulson & Wright 1998) exhibit this behavior. Darwin (1876) implied that constancy of insect pollinators was a result of a forager's inability to switch efficiently amongst several different flower-handling skills over a relatively short period of time.

"*That insects should visit the flowers of the same species for as long as they can, is of great importance to the plant, as it favours cross-fertilization of distinct individuals of the same species, but none will suppose that insects act in this manner for the good of the plant. The cause probably lies in insects thus being able to work quicker; they have just learned how to stand in the best position on the flower and how far and in what direction to insert their proboscides*" (Darwin 1876, p.419).

According to this theory, insect nectivores were expected to experience an increase in flower handling time immediately following a switch in flower types (Waser 1983). This idea is supported by Lewis' (1986) study of the foraging behavior of the butterfly *Pieris rapae.* Learning the flower handling technique of one plant species interfered with previously learned flower handling methods, and individual butterflies tended to stay constant to flowers of the plant species that they had most recently visited.

> Indeed, if flower-constancy evolved in mountain regions with a sequential flowering pattern, flower constancy would seem an appropriate strategy because plants here often occur as a series of non-overlapping single-species nectar resources (Waser & Real 1979). Only on rare occasions would a forager in this environment experience a situation that would elicit natural selection for flower choice. As nearest flowers are conspecifics and little floral variety exists at one time, in fact, it would be most efficient for a forager to only exhibit specialization (Waser & Real 1979).
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> Nevertheless, research on the skipper butterfly species *Thymelicus flavus* shows that despite exhibiting 85% fidelity to one plant species, these butterflies ignored most of the flowers of this plant species that they encountered (Goulson *et al.* 1997). Further, flower fidelity did not appear to be the result of prior experience gained on the handling of one particular flower type. Obviously, our understanding of the forager's decision process is not complete.
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> In addition, bumblebees can efficiently master the task of handling two different flower types when trained to do so on artificial flower patches (Chittka & Thomson 1997). In this case, foragers did not experience an increase in handling-time every time they switched flower types in the experiment. In a field situation, Laverty (1993) similarly found that bumblebees exhibited no tendency towards flower constancy when foraging on simple flowers where there were no fundamental increased handling-time or costs (longer flower corollas) associated with a certain flower type. However, bumblebees foraging on more morphologically diverse flower species showed strong constancy, which was correlated to

increased handling-time and error rate associated with some flower types.

Thus, flower fidelity does not appear to be readily explainable by a forager's inability to learn multiple tasks – at least in situations where flower morphology does not differ too greatly.

III. Energetic Considerations?

a) *Individual Constancy*

Individual constancy has been coined as a term to describe the persistent foraging behavior of a honeybee to flowers of a single color irrespective of the reward gained when different bees exhibit extreme fidelity to different flower colors. Since workers visiting blue flowers show the same level of fidelity as those visiting yellow flowers, individual constancy cannot be ascribed to species-level innate-color preference in honeybee foragers.

Given that flower color choices at a location exist, energy maximization theory predicts that flower fidelity should be to the flower type offering the greater reward. In the simplest scenarios, where either a difference in reward quantity or quality is offered by competing plant species, bees should choose the flower type associated with the greater quantity or quality reward. However, offering honeybees over a two fold reward quality difference (0.75 vs. 2.0M), or even ten fold difference in reward volume (2 vs. 20ul), when associated with yellow and blue flowers does not weaken the flower fidelity of the honeybee forager (Wells & Wells 1983). Moreover, this flower fidelity of honeybees is not a simple matter of color attractiveness because ***some foragers limit visitation to yellow flowers and others to blue flowers in a patch***, even though bees are visiting the same flower patch at the same time when rewards offered by the competing flower colors are not equal.

Obviously, this type of flower fidelity can be energetically inefficient for an individual bee because the flower color preference persists despite differences in reward quality or quantity (Wells & Wells 1983). Still, the possibility existed that the fidelity exhibited by individual bees was due to learning during prior foraging experiences, and re-learning is difficult for foragers. That question was answered by repeating the above study but with bees that had never foraged, or even been outdoors (Cakmak & Wells 1995). Flower color fidelity was just as intense. Again, some bees specialized on blue while others specialized on yellow irrespective of difference in reward offered by the two flower colors. Although this evidence seems conclusive, honeybee forager information processing has yet another level of complexity.

b) *Context Dependent Decisions*

Research has now shown that honeybee foraging behavior does not always follow the individual-constancy prototype described. In specific situations, flower-constant foraging behavior is maintained during visits to a flower patch irrespective of rewards, while in other situations honeybees will forage to optimize the reward gained (Wells & Wells 1986; Hill *et al.* 1997). That is, when considered from a psychological perspective, forager flower choice is dependent on the context in which it is offered (Shafir 1994).

On a patch of artificial flowers honeybees exhibit two distinctive behavioral responses to a disparity in flower color. First, when given a choice of flower colors distinctive in the bee's color space (perception of color: Chittka 1992), such as blue versus yellow flowers, a forager will visit only blue flowers or only yellow flowers. In fact, pre-training bees by forcing each to visit both yellow and blue flowers is of no consequence to an individual bee's flower fidelity. As soon as flower choice is restored in the experiment individual constancy reappears spontaneously (Hill *et al.* 1997). Second, when presented a choice of colors of similar spectral reflectance, such as blue versus human-white (lacking UV) flowers, flower choice is based on caloric reward even when different sugars are involved (Wells *et al.* 1992). Hence, in this situation, random flower selection is observed when rewards are equal, and fidelity to the flower color offering the greater caloric reward occurs when the rewards are not equal. This second observation is in accordance with optimal foraging theory: it predicts that during the search for nectar, the behavior exhibited by a bee maximizes net energy gain (calorie gained per calorie expended), and thus given that the energy spent foraging on different flower types is equal then a bee will choose the flower type with the greater reward (Stephens & Krebs 1986). Thus, flower fidelity of honeybees can also result from reward differences among flower types, but unlike individual constancy all bees choose to visit the same type of flower when choices exist.

The significance of context dependent decision processes to honeybee foraging is not confined to flower-color combinations. For years the existence of individual constancy behavior was questioned because the results of similar experiments with blue and yellow flower choices in different laboratories were inconsistent (*e.g.*

Waddington & Holden 1979; Marden & Waddington 1981). We now know that the differences in results are due to a slight difference in artificial flower design that affects spatial positioning and, as a consequence, foraging strategy. Giving bees blue and yellow flowers to choose between results in individual constancy if flowers are pedicellate (have stems) so that bees must fly from flower to flower. Yet, behavior consistent with energy maximization theory is exhibited if flowers simulate an inflorescence (bee-board design flower patch) where bees can walk from flower to flower (Wells & Wells 1984).

> We suspect that flower-based color, color-pattern (such as nectar guides), and flower morphology differences are also providing the basis for context dependent decisions where in the past a simple color has been considered to be the sole factor involved in honeybee flower choice. Two basic changes in the way the behavior of honeybees must be viewed have been brought about through the study of context dependent foraging.

- First, honeybees obviously can, and do under some contexts make decisions about which flowers to visit based on volume and molarity of rewards offered by competing flower types. Thus, honeybees ***are mentally capable of comparison of rewards associated with different flower types*** (*e.g.* Wells & Wells 1986; Waddington & Gottlieb 1990; Wells *et al*. 1992; Hill *et al*. 2001), but under some contexts do not utilize this type of information, and that results in individual constancy behavior (*e.g*. Wells & Wells 1983; Hill *et al*. 1997; Sanderson *et al*. 2004).

- Second, the differing conclusions about honeybee foraging behavior that prevail in the literature should not necessarily be viewed in terms of which is correct, but rather in terms of the question: ***are there differences in the context under which the same choice was presented***? This may be extremely important for agriculture in the future, since simple changes in flower color or color-pattern may yield very different results in terms of hybrid seed production.

c) *Handling-Time*

Unlike the situation discussed where increased foraging time was associated with how experienced a forager was with different tasks that yielded roughly the same nectar reward, flower morphology differences also can create variation in harvest rates that surpass what can be compensated for by learning (Laverty 1994). As discussed above, factors such as nectar sugar-content are used as a measure of reward by a honeybee, and under some contexts determine flower fidelity. However, how long it takes to retrieve a specific reward can be as important as the reward itself, and may in fact be a significant factor in explaining flower fidelity in some situations (calories/second).

Time related factors do seem to be used in foraging decisions by bees. In a study by Schmid-Hempel (1984) on the importance of handling time on the flight directionality of the honeybee, handling time influenced the direction in which a bee moved between flowers. Short handling times resulted in continued movement though the flower patch in the same direction, but upon visiting a flower with a higher handling time bees tended to change directions. Two reasons were suggested for this behavior: 1) with the longer handling time a forager forgot the direction in which it was traveling, or 2) bees were trying to stay in an area of higher reward. The significance of this experiment is that it shows the importance of handling time, even though no color choice was given. However, since handling time was controlled by reward volume, the data cannot be used to support one explanation over the other**.**

In experiments by both Waddington & Gottlieb (1990) and Sanderson *et al.* (2004), handling time has been separated from reward. Waddington & Gottlieb (1990) completed a honeybee choice experiment with tubular flowers where they varied well depth by inserting false bottoms into the tubes. Hence, from the outside it would have been impossible to observe a difference in tube depth, but tube depth was linked to flower color. Bees chose the flower color with the shorter handling time (shallow wells). Again, these results are context dependent (Sanderson *et al.* 2004), and thus individual constancy will result with some flower color dimorphisms and/or flower color-patterns. Of further significance, Sanderson demonstrated that bees were using a comparative rather than absolute measure of reward. That is, they were not actually calculating calories/second.

In a more complex situation, travel distance was dissociated from reward. Hill *et al.* (2001) determined whether or not color cues are superceded by energy constraints in the honeybee by varying the reward and distance between flowers. Flowers were placed in adjacent pairs, where paired flowers were of differing color. A bee had to travel a much greater distance to visit flowers of the same color. They found that with blue and white flowers when the rewards were equal the bees visited the closest flower, thus exhibiting energy maximization behavior. However, they traveled further to harvest a higher net caloric reward (calories/sec.)

when reward quality differed between close and far flowers. Yet, in true context dependent behavior, results corresponded to individual constancy behavior when a yellow-blue dimorphic flower patch was used. Here bees visited the closest flowers only 5% of the time, and even when reward was varied no behavioral differences were recorded (Hill *et al.* 2001). The above experiments suggest that neither flower handling-time nor travel-time is a factor in individual flower constancy behavior.

Thus, handling and flight times can result in honeybee flower fidelity, just as differences in reward quality and quantity. However, flower fidelity can instead result from individual constancy in which case effort involved does not influence flower fidelity.

d) *Dynamic Environments*

Fidelity to the plant species offering the greater reward will necessarily result in depletion of its reward, thus a lower rewarding flower type will eventually become more rewarding. In order to harvest nectar from the environment efficiently forager distribution should mirror the productivity of the different flower types, which should produce the Ideal Free Distribution of flower visitation by foragers (Fretwell & Lucas 1970). Bumblebees appear to deal with dynamic environments by ‘majoring’ and ‘minoring’ (Heinrich 1979). That is, bumblebees systematically exploit flowers of one type, but on a less regular basis visit other types of flowers, and thus show less flower fidelity than honeybees (*e.g.* Grant 1950). Honeybees appear to deal with dynamic environments through recruitment (Wenner & Wells 1990) and individual constancy foraging behavior (Wells & Wells 1983) rather than ‘majoring’ and ‘minoring’ (Marden & Waddington 1981). Thus, honeybee flower fidelity is very high. Nevertheless, there may be rare contexts where honeybees temporarily major and minor when foraging (Greggers & Menzel 1993)

IV. Non-Visual Cues?

Visual cues, particularly color, play an important role in the flower fidelity of honeybees as shown in the preceding discussion. In some situations, foragers learn to associate a particular flower color with a greater net reward, and in other cases flower color difference triggers individual constancy where each bee has high fidelity to one color of flower but different bees limit visitation to different flower colors. However, visual stimuli (such as color) are not the only cues honeybees use to make foraging decisions.

Just as foragers can learn to associate flower color with a reward and then show fidelity based on flower color, ***foragers also can rapidly learn to associate flower or nectar odor with a reward*** in a simple conditioning manner (Wenner & Johnson 1966; Bitterman *et al.* 1983; Abramson 1994). When presented a flower patch that had an odor dimorphism, in fact, some bees limited visitation to flowers with a particular scent (Wells & Wells 1986b).

Honeybee foragers may often be pre-trained to a scent before ever leaving the hive (Wenner & Johnson 1966; Johnson 1967; Wells & Rathore 1994b; Reinhard *et al.* 2004), which in itself can initiate flower fidelity. Giurfa *et al.* (1995) examined flower color choices of honeybees that had no prior experience with natural flowers and found that these bees were never attracted by a color stimulus unless they had been previously given a scented reward associated with a particular color. Therefore, color alone does not facilitate a bee’s first encounter with the flower. Some have thus argued that color is not the key factor in the flower fidelity of honeybees (Greggers & Menzel 1993; Shafir 1994). Despite this, color is still considered to be the most important cue for the detection and recognition of flowers at a distance and must be the primary cue when a series of rapid decisions are made (Chittka & Menzel 1992).

V. Subspecies Variation?

When presented a flower patch where choices are between blue and yellow flowers, some *Apis mellifera ligustica* foragers first land (by chance) on yellow, others on blue. Each bee shows remarkable fidelity to its first color choice (Wells & Wells 1983). Further, individual based flower fidelity is independent of forager experience (Cakmak & Wells 1995), and very resistant to training (Hill *et al.* 1997). However, that very-high degree of individual based flower color fidelity does not appear in Africanized bees, *A.m. scutellata*, where energetic considerations weaken this type of flower fidelity (Cakmak *et al.* 1999). Thus, the legendary ***flower fidelity of honeybees appears to be somewhat subspecies dependent***, and probably also varies among *Apis* species.

Two potential reasons for subspecies variation in flower fidelity are predation and parasitism risk, as observed in bumblebees (Cartar & Dill 1991). In fact, when comparing the individual based flower fidelity of *A. mellifera* subspecies from different habitats in Turkey

(*Am. armeniaca*, *A.m. caucasica*, *A.m. cypria*, and *A.m. syriaca*) a correlation between predatory wasp prevalence and honeybee foraging behavior existed (Cakmak & Wells 2001). In those regions where wasps are common, *Apis* mortality as a result of predation is considerable (Ozbeck 1982; Evans & O'Neill 1988; Sharma & Raj 1988; De Jong 1990). Honeybee subspecies endemic to those high-predation regions tend to show less flower fidelity that is irrespective of reward (Cakmak & Wells 2001) than do honeybee subspecies endemic to regions with little or no honeybee predation (Banschbach & Waddington 1994; Fulop & Menzel 2000). Support for that relationship is observed in studies involving some ant species (Nonacs & Dill 1988, 1990; Nonacs 1990). Presumably, prey that are foraging should use resources in a manner that minimizes predation-risk (Greene 1986; Gilliam & Fraser 1987; Brown 1992), and that may involve gathering nectar irrespective of quality.

However, before any definitive conclusions can be reached, much more work is needed to sort out counter claims that starvation risk may actually be the key factor in forager flower fidelity (Real 1981; Harder & Real 1987), or that even a functional response to immediate predation-risk alters flower fidelity of foragers.

VI. CONCLUSIONS

The legendary flower fidelity of honeybees actually arises for different reasons. Like many other species, honeybee flower fidelity can arise from energetic considerations involving nectar reward quality, quantity or work considerations (flower handling time or distance between flowers). Evidence suggests, however, that information processing is comparative rather than absolute. That is, while they can use each of those types of reward information, when two or more of those reward characteristics vary simultaneously honeybees cannot truly combine that information into a single statistic (*e.g*. calories/second). Honeybees can also use reward frequency to restrict flower visitation when reward frequency creates a difference in average reward between two flower types (*e.g*. Wells & Wells 1986). At present, whether honeybees use differences in frequency when average rewards are equal (risk-sensitivity) in competing flowers is controversial (*e.g.* see: Banschbach & Waddington 1994; Cakmak *et al.* 1999; Fulop & Menzel 2000; Cakmak & Wells 2001; Shafir *et. al.* 1999). The advantage of basing flower fidelity on energetic considerations is obvious in terms of survival and reproduction, and thus is expected evolutionarily. At the colony level, efficiency of scout bees (bees finding a new nectar source for the colony) may be crucial. The time it takes for these first few bees from a colony to find a new nectar location in the environment is very long, whereas recruitment of naïve bees by experienced foragers to that location is quite rapid (Frisch 1950). Recruitment appears to be more than simply getting naïve bees to visit a new locality, pre-training of naïve foragers to an odor occurs (Frisch 1939, 1943; Wenner & Johnson 1966; Johnson 1967; Reindhard *et al.* 2004) and thus can lead to flower fidelity not based on energetic considerations. When overall harvest rate for the colony is considered, the time saved by each naïve bee rapidly finding a nectar source may very well more than compensate for a bee's harvest rate once a nectar source is found, and thus be selected on a colony level since net reward is greatest (calories/time).

What is interesting about the flower fidelity of honeybees is that flower constancy also arises from non-energetic considerations that can take precedence over energetics in the decision making process of foragers. Flower fidelity can be the result of individual constancy behavior. Here each forager shows extreme fidelity to one flower type irrespective of reward, but different individuals specialize on different flower morphs. Why honeybees exhibit flower constancy remains unresolved (Goulson *et al.* 1997, Hill *et al.* 1997) despite the amount of empirical evidence that has been accumulated. Individual constancy seems inconsistent with animal foraging theories (Wells & Wells 1983), yet exists. Among the suggested evolutionary benefits are: 1) Sibling interference will be lowered in a flower patch (Wells & Rathore 1994), 2) Rather than optimization, interference competition drives evolution of forager behavior. In this case, a colony attempts to take all the nectar resource, which negatively affects competing nectivore species (Hill *et al.* 1997), and 3) Plant fitness is improved by limiting pollen waste within a plant community (Grant 1949) through individual constancy of foragers (Wells & Wells 1986), and that leads to greater nectar resources. However, none of these models currently have much empirical support. Thus, at this time, from an evolutionary viewpoint individual constancy remains an enigma.

What is now especially intriguing is the extent of the role context dependence plays in determining the type of flower fidelity observed. Seemingly inconsequential changes in flowers morphology produce extreme changes in forager behavior. That may be a blessing for agriculture -changing honeybee forager behavior may not be the daunting task it at first appears, especially when honeybee subspecies variation in foraging is also considered. Perhaps now our biggest challenge is to understand the context dependent nature of each type of flower fidelity exhibited by the honeybee forager.

VII. REFERENCES

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