Reward Frequency: Effects on Flower Choices Made by Different Honeybee Races in Turkey*

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Abstract: We compared the European honeybee races *Apis mellifera armeniaca*, *A.m. caucasica*, *A.m. cypria*, and *A.m. syriaca*. These subspecies are endemic to very different habitats. Additionally, they are exposed to very different levels of predation. *A.m. caucasica* exists where honeybee predators typically are rare, while the remaining subspecies have ranges that coincide with areas where honeybee predators are abundant. Foraging decisions of workers visiting artificial flower patches containing blue, white, and yellow flowers were recorded. We tested whether foragers responded to differences in rewarding flower frequency among flower color morphs. Division of labor occurred among foragers of each race; some bees frequented yellow flowers while other bees from the same hive visited blue and white flowers. *A.m. caucasica* foragers ignored differences in reward frequency among flower colors. Even bees that frequented blue and white flowers did not base flower choice on reward frequency differences between just these two color morphs. In contrast, *A.m. armeniaca*, *A.m. cypria*, and *A.m. syriaca*, however, did respond to differences in reward frequencies, tending to avoid the less frequently rewarding flower color morph. *A.m. armeniaca* forager division of labor (foragers committed to yellow or to blue and white flowers) was dominant to energy maximization. The reverse was true for *A.m. cypria*.

Key Words: *Apis mellifera* races, honey bees, foraging, prey-predator relationship, artificial flowers

Nektar Sıklığının Türkiye'de Bulunan Farklı Bal Arısı Irklarının Çiçek Tercihleri Üzerindeki Etkileri

Özet: Bu çalışmada Avrupa arı ırklarından *Apis mellifera armeniaca*, *A.m. caucasica*, *A.m. cypria*, ve *A.m. syriaca* karşılaştırılmıştır. Bu ırklar çok farklı habitatlara adapte olmuşlar ve farklı derecede predatör etkisi altındadır. Genel olarak *A.m. caucasica*'nın yaşadığı bölgede predatörler azdır, buna karşılık diğer ırkların yaşadığı bölgelerde bal arısı predatörleri daha yaygındır. Mavi, beyaz ve sarı çiçekleri ziyaret eden yayılmacı arıların çiçek tercihleri kaydedilmiştir. Yayılmacı arıların çiçek renkleri arasında nektar sıklığına olan reaksiyonları test edilmiş ve her ırkın yayılmacıları arasında bir işbölümü mevcuttur. Aynı kovandaki bazı arılar sarı çiçekleri, diğerleri mavi ve beyaz çiçekleri tercih etmişlerdir. *A.m. caucasica* yayılmacıları çiçek renkleri arasındaki nektar sıklığına bağlı riski dikkate almamışlardır. Mavi, beyaz çiçekleri tercih eden yayılmacılar bile çiçek tercihlerini nektar sıklığını dikkate alarak yapmamıştır. Bunun aksine *A.m. armeniaca*, *A.m. cypria*, ve *A.m. syriaca* nektar sıklığına bağlı riske reaksiyon göstermiş, sürekli nektar bulundurmayan çiçeklerden kaçınmışlardır. A.m. armeniaca' da arılar arasındaki işbölümü (sarı, mavi ve beyaz çiçeklere bağımlı yayılmacılar) enerji maksimasyonuna göre daha güçlüdür. Bunun tersi *A.m. cypria*'da görülmüştür.

Anahtar Sözcükler: *Apis mellifera* ırkları, bal arıları, yayılma, prey-predatör ilişkisi, yapay çiçekler

Introduction

European honeybees (*Apis mellifera*) are found in deserts, tropical forests, temperate savannas, and mountain regions. They occur from sea level to 2000 meters elevation, and are found on every continent except Antarctica (1). The physical environment and seasonality vary tremendously among the habitats where *A. mellifera* are found. Morphological differences in the European honeybee mirror the habitat diversity *A. mellifera* occupies (2,3). Differentiation within *A. mellifera* includes coloration, overall worker body size, gross anatomical features such as tongue length, and isozyme diversification (1,4). Average colony size also varies predictably among subspecies (1). There are at least 24 morphological races of *A. mellifera* (1). Behavioral response differences to specific stimuli also exist among

European honeybee subspecies. Genetically based differences in aggressiveness and hive-defense reactions are well documented. Along with the hive defense and aggression differences that exist among the European honeybee subspecies, we suspect that marked forager flower fidelity differences also exist among *A. mellifera* races.

Our picture of honeybee foraging stems primarily from studies of the few subspecies endemic to Western Europe which were imported to the Americas. Those foragers visit a wide range of flower types but invariably become "crop attached" (5-7). That is, each forager not only returns repeatedly to the same location to gather nectar and pollen but also returns to the hive with only one plant species of pollen (6,8,9). This flower fidelity occurs even when alternative flower choices exist at a foraging location (10,11), so it cannot be explained by lack of flower choices.

Flower constancy, where an individual forager actually bypasses rewarding flowers to restrict visits to a single plant species (12,13), is spontaneous in the Italian honeybee (14). When free flying bees, naive to the experimental apparatus, are offered rewards simultaneously from yellow and from blue flowers, they choose one color flower morph to which they become constant, rarely even sampling the alternative. However, some bees will restrict visitation to yellow while others from the same colony will restrict visitation to blue flowers (14). This fidelity to a single flower color not only occurs in experienced foragers (15) but also in naive bees caged since eclosion (16). In fact, individuals continue to choose the initial color visited even when it is un-rewarded after the first visit (17) and this cannot be explained using energy maximization principles (18). Although substantial literature exists concerning attempts to explain the paradox in constancy behavior, a single mechanism has not been found (13).

However, flower constancy behavior in European honeybees is not observed with all experimental flower color combinations. When blue flowers and white flowers are present in the same flower patch and offer equivalent caloric rewards, each honeybee forages, visiting each of these flower colors extensively. These same foragers will switch to the flower color morph offering the higher caloric content nectar when a difference in rewards exists between blue and white flowers (19). Thus, honeybee flower fidelity is not the result of memory limitations or inability to make reward comparisons between flower color morphs. Although energy maximization principles explain honeybee behavior on flower patches of blue and white flowers, Italian honeybees do not respond to differences in the frequency of rewarding flowers among alternative floral morphs, presumably because of their colony size (15,18,20, because bumble bees actually respond to differences in the frequency of rewarding flowers among alternative floral morphs (21-23).

We conducted a comparative study of *Apis mellifera armeniaca*, *A.m. caucasica*, *A.m. cypria* and *A.m. syriaca* foraging when only the frequency of rewarding flowers differed among sympatric floral types. These subspecies are endemic to very different habitats (1). Additionally, *A.m. caucasica* was observed in a region where specialized bee predators are rare, while the remaining races were studied where bee predators are common.

Materials and Methods

The study involved four races of *Apis mellifera*: *A.m. caucasica* was studied near Tirebolu, Turkey, on the eastern Black Sea (steep forested mountains with a cool rainy climate), *A.m. syriaca* at Şanlıurfa, Turkey, near the Syrian-Turkish inland border (arid Harran Valley), *A.m. cypria* in Girne, Turkish Cyprus (subtropical climate), and *A.m. armeniaca* in the mountains surrounding Kars, Turkey, on the Turkish-Armenian border (a region of short, hot summers and long, cold winters). *A.m. caucasica* is known as a gentle bee that lacks an aggressive hive defense (1). The other three races are more aggressive and have energetic hive defenses (1,24, 25).

Subspecies were identified using morphological traits. Initial identification of specimens was established by M. Çiftçi (agricultural engineer) and C. Semseddin (beekeeper), and Dr. Alexander of the University of Kansas, USA, independently verified subspecies identifications.

Specialized bee predators are not common, and none were observed where *A.m. caucasica* was studied. *Vespa orientalis* were frequently observed attacking honeybees in front of the hive, and they often captured honey bee foragers visiting flowers (natural and artificial) in Cyprus and in the Harran Valley. *Vespa crabro* around Kars, and *Philanthus triangulum* in the Harran Valley, were often seen preying on honeybees foraging on flowers. Honeybee mortality from predation is a major apicultural

problem in the regions inhabited by Armenian, Cyprus, and Syrian bees (26).

Bees, in each case, were trained to visit a watch glass provisioned with 10µl/L clove-scented 1M sucrose solution located 150m from the hive. The watch glass was replaced with an artificial flower patch and bees were allowed to freely choose which flowers to visit. The studied bees were individually marked. All other bees were removed and caged.

The artificial flower patches contained 12 blue, 12 white and 12 yellow pedicellate flowers randomly arranged as to color [for further detail and reflectance spectra see (18)]. Flowers within a patch were rearranged between treatments and periodically within treatments. The color of every flower visited by each marked bee was recorded.

The experiment with each *A. mellifera* race consisted of four treatments performed sequentially and without interruption in a repeated measures experimental design (27). Treatment 1: all flowers contained 5µl unscented 1M sucrose reward. Treatments 2: two-thirds of the blue flowers were empty and one-third contained a 5µl unscented 1M sucrose solution, while all white and yellow flowers had 5µl unscented 1M sucrose reward. Treatments 3 and 4 were identical to Treatment 2 except that the test flower color for Treatment 3 was white (all blue and yellow flowers with reward) and for Treatment 4 was yellow (all blue and white flowers with reward). Flowers with a reward were refilled as they were emptied with 5µl unscented 1M sucrose solution.

Reward volumes offered were in the range commonly used in honey bee experiments (e.g., 28: 2µl; 29: 5µl). Further, we have shown that neither Italian bee blue-white flower choice nor constancy to blue or yellow flowers is influenced by reward quantities in the range of 2µl to 100µl (14,15,18). In fact, Greggors and Menzel (30) report loss of honey bee flower fidelity with the use of 1µl reward; perhaps foragers continue visiting a flower type only if some rewards exceed 1µl.

Data from each subspecies of honeybee were analyzed separately. The following procedure was used for data analysis in each case (i.e., for each subspecies).

The behavior of Italian bees led us to assign each bee to a statistical group based on the first flower a bee visited. Each Italian forager spontaneously limits visitation to only yellow flowers or to only blue and white flowers,

regardless of rewards. Thus, two groups were defined for bees tested in each experiment. The yellow-group was composed of those bees that first visited a yellow flower. The not-yellow group was composed of those bees that first visited either a blue or a white flower. This grouping of bees allowed us to examine whether initial flower color visited by a bee is a predictor of subsequent flower color choices [as reported for Italian bees by Hill et al. (14)] and/or influenced whether reward frequency associated with each flower color is used in subsequent flower color choices.

The statistical analysis was based on the frequency of white flowers visited by each bee in each treatment. That decision was made because the proportion of white flowers visited, by itself, (or proportion of blue flowers visited by itself) is sufficient to describe the Italian bees flower visitation. Italian bees of the yellow group very rarely visit white flowers (or blue flowers) while Italian bees of the not-yellow group frequent both white and blue flowers but ignore yellow flowers.

Data were analyzed using a Repeated Measures MANOVA (27). A group by treatment statistical design was employed. That is, we tested for the effect of the flower color first visited by a bee (bees assigned to the yellow or not-yellow group) and for the effect of reward frequency in different flower types (the different treatments had a different flower color with the variable reward). Data were transformed before analysis by taking the arcsine square-root of the proportion of white flowers visited in each treatment. That transformation normalizes proportions for either ANOVA or MANOVA data analysis (27).

Results

Observations were made on 5979 flower choices by 12 Caucasian foragers from 3 colonies (Fig. 1) *A.m. caucasica*, the subspecies without major predation pressure, based flower choices on the first flower color a bee visited (no group effect: $F=609.0$; $df=1,10$; $P<0.0001$), but did not respond to differences in reward frequency that existed among flower types (no treatment effect: $F=0.85$; $df=3,8$; $P<0.50$). Further, whether a bee first visited a yellow or first visited either a blue or white flower did not affect whether reward frequency was used to make flower visitation choices (no interaction effect
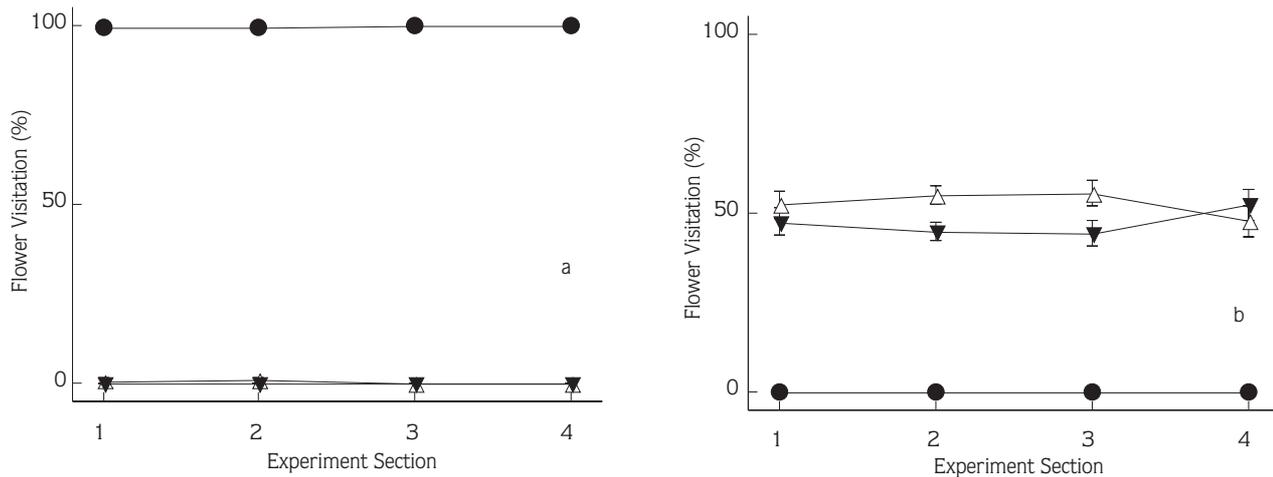
Figure 1.   *Apis mellifera* caucasica forager response to changes in reward frequency associated with flower color morphs (blue, white and yellow). Percent visitation (mean and standard error among bees) to each flower color (• = Yellow, = ▼ Blue, △ = White) by experimental section is given for bees first selecting a yellow flower (Fig. 1a) and for bees first selecting either a blue or white flower (Fig. 1b). Reward frequencies do not differ among flower color morphs in section. Blue flowers offer a less frequent reward in section 2, white flowers in section 3, and yellow flowers in section 4. Specialized bee predators were not seen during the experiment, and are rare in the region inhabited by Caucasian honeybees.

between group and treatment: F=0.29; df=3,8; P<0.83). These results correspond closely to behavior of the Italian bee (14,18). This behavior has been suggested to increase forager efficiency though division of labor among workers (31), possibly by reducing interference (32). In terms of pollination ecology, this behavior minimizes cross pollination between flowers of some colors and thus can create sympatric isolation of plants based on flower color alone (11).

On the other hand, the three subspecies endemic to regions where honey bee predation is an apicultural problem each exhibited a significant treatment effect (*A.m. armeniaca*: F=10.1; df=3,10; P<0.0023; *A.m. syriaca*: F=19.5; df=3,9; P<0.0003; *A.m. cypria*: F=16.3; df=3,9; P<0.0006), as well as a group effect (*A.m. armeniaca*: F=109.8; df=1,12; P<0.0001; *A.m. syriaca*: F=245.3; df=1,11; P<0.0001; *A.m. cypria*: F=32.8; df=1,11; P<0.0001). Additionally, there was a significant treatment x group interaction (*A.m. armeniaca*: F=4.9; df=3,10; P<0.023; *A.m. syriaca*: F=11.3; df=3,9; P<0.0021; *A.m. cypria*: F=9.95; df=3,9; P<0.0032). That is, foragers of each subspecies that first visited a blue or white flower limited visitation to blue and white flowers, but would avoid blue flowers if blue offered rewards less often than white flowers and avoid white flowers if white offered rewards less often

than blue flowers. Conversely, bees that first visited a yellow flower continued to highly favor yellow flowers. These overall trends, however, mask subspecies defined differences in behavior exhibited by bees favoring yellow flowers (see the Discussion section). These results show significant differences from the behavior exhibited by the Italian bee (e.g., 14,18). The analyses are based on 12,050 flower choices by 14 Armenian bees from 3 colonies (Fig. 2), 9738 flower choices by 13 Syrian bees from 3 colonies (Fig. 3), and 3589 flower choices by 13 Cyprus bees from 2 colonies (Fig. 4).

Discussion

The differing behavior of honeybee foragers we describe may be the result of different predation pressures. Where specialized *Apis* predators are common, honeybee forager flower choice should minimize predation-risk while maximizing harvest rate (33). The beewolf (*Philanthus triangulum*) Oriental wasp (*Vespa orientalis*), and European wasp (*Vespa crabro*) are specialized bee predators. In regions where they are common, *Apis* mortality as a result of predation is considerable (34-36). Responses of *Apis* to predators attacking the hive (queen, brood and food stores threatened) are well documented (e.g., 1,37). However,
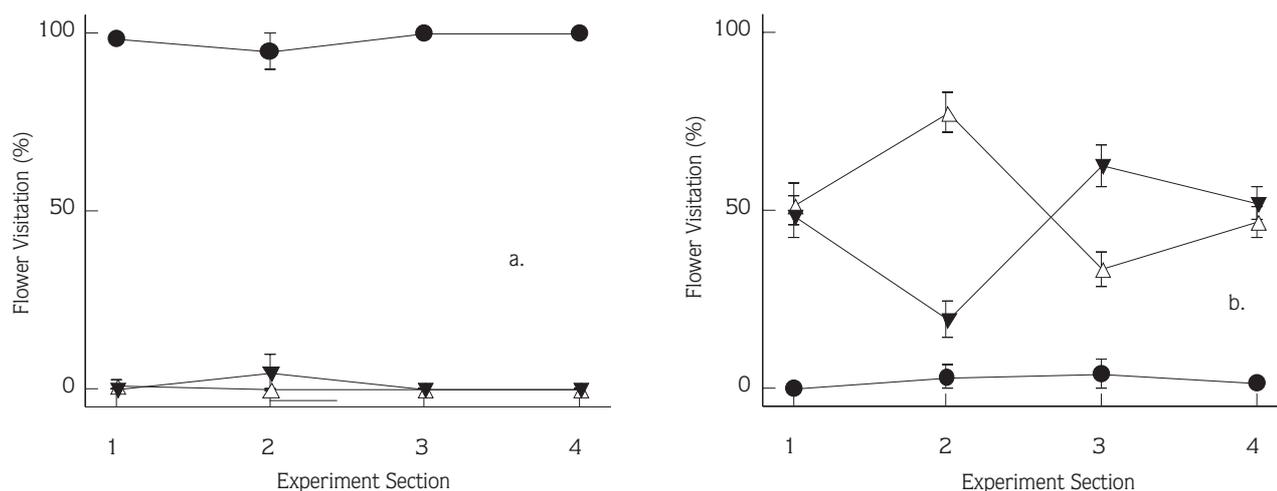
Figure 2.   *Apis mellifera armeniaca* forager response to changes in reward frequency associated with flower color morphs (blue, white and yellow). Percent visitation (mean and standard error among bees) to each flower color (• = Yellow, = ▼ Blue, △ = White) by experimental section is given for bees first selecting a yellow flower (Fig. 2a) and for bees first selecting either a blue or white flower (Fig. 2b). Reward frequencies do not differ among flower color morphs in section 1. Blue flowers offer a less frequent reward in section 2, white flowers in section 3, and yellow flowers in section 4. *Vespa crabro* was common at the experimental site and throughout the region inhabited by Armenian honeybees.
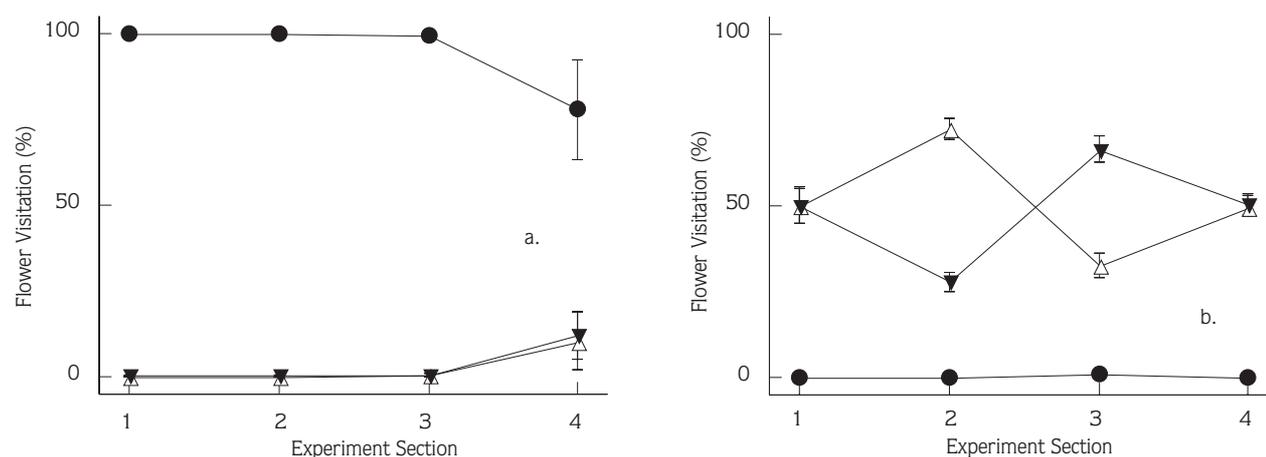

Figure 3.   *Apis mellifera syriaca* forager response to changes in reward frequency associated with flower color morphs (blue, white and yellow). Percent visitation (mean and standard error among bees) to each flower color (• = Yellow, = ▼ Blue, △ = White) by experimental section is given for bees first selecting a yellow flower (Fig. 3a) and for bees first selecting either a blue or white flower (Fig. 3b). Reward frequencies do not differ among flower color morphs in section 1. Blue flowers offer a less frequent reward in section 2, white flowers in section 3, and yellow flowers in section 4. *Vespa orientalis* and *Philanthus triangulum* were common at the experimental site and present a major apicultural problem throughout the region inhabited by Syrian honeybees.

behavioral adaptations to non-incident related predation threat away from the hive, such as risk-sensitive foraging, have not been reported.

Caucasian honeybees did not alter flower choice in response to differences in rewarding flower frequency correlated with flower color, not even between blue and white flowers (Fig. 1). However, some bees limited visitation to yellow and other bees avoided yellow flowers regardless of treatment. As with ants, forager specialization reduces intra-colonial competition (38,39) and perhaps is more important than energy maximization. These behaviors are characteristic of Italian honeybees (14,15,18), and are also consistent with
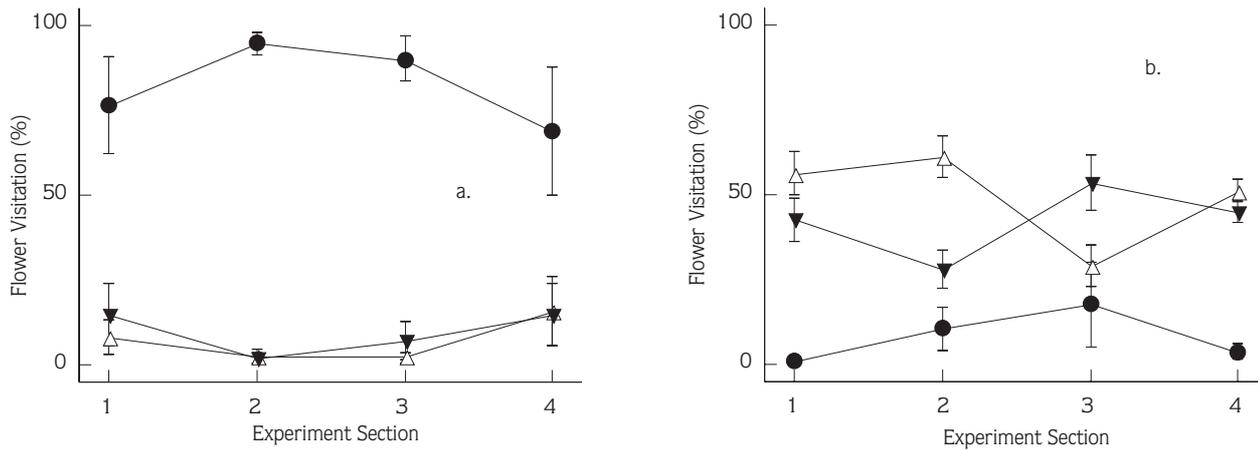
Figure 4. *Apis mellifera* cypria forager response to changes in reward frequency associated with flower color morphs (blue, white and yellow). Percent visitation (mean and standard error among bees) to each flower color(• = Yellow, = ▼ Blue, △ = White) by experimental section is given for bees first selecting a yellow flower (Fig. 4a) and for bees first selecting either a blue or white flower (Fig. 4b). Reward frequencies do not differ among flower color morphs in section 1. Blue flowers offer a less frequent reward in section 2, white flowers in section 3, and yellow flowers in section 4. *Vespa orientalis* was common at the experimental site and present a major apicultural problem in Cyprus.

predation-risk foraging decisions since specialized bee predators were rare (33,40, model expects bees to minimize the ratio u/f but since u=[predation-risk]=0 then u/f=0 for all f>0).

In contrast, specialized bee predators were common at the sites where the Armenian, Cyprus and Syrian honeybees were studied and, in each case, forager avoidance of the color morph with fewer rewarding flowers was noted (Figs. 2, 3 & 4). Foragers frequenting blue and white switched between the two colors in a manner that avoided the color morph with fewer rewarding flowers (Figs. 2b, 3b, 4b). However, the behavior of bees frequenting yellow flowers differed among the three races. Armenian bees were indifferent while Cyprus bees were sensitive to a decrease in the frequency of rewarding yellow flowers (Figs. 2a & 4a). Apparently, forager specialization among foragers was dominant to energy-maximization or predation-risk based foraging decisions in *A.m. armeniaca*.

Prior studies have reported that honeybees do not respond to differences in rewarding flower frequency in competing flowers, even between blue and white flowers (15,18), and even when manipulating hive energy resources (20). On the other hand, bumblebee foragers are generally risk-averse; avoiding less frequently rewarding flower types maximizes the rate of energy harvest (21,41). However, manipulation of bumblebee

colony energy resources can lead to risk-prone foraging (22). Short-term negative energy budgets alone do not appear to be critical since bumblebees compensate by lowering colony temperature (42). But altered colony defense behavior associated with lowered colony temperature increases bumblebee susceptibility to predators, providing the foundation upon which risk-sensitive foraging decisions are based (42).

Honeybee foraging decisions have not previously been studied in regions where predation markedly affects forager survival. Where abundant, beewolves and wasp predators are capable of decimating a honey bee hive within a few days (36,43). The study sites of *A.m. armeniaca*, *A m. cypria* and *A.m. syriaca* were located in areas where specialized bee predators are an acute problem currently (1,25,26,34), and a historical apicultural problem dating from at least the Roman Empire (44). Loss of honeybees from predation while workers foraged on artificial flower patches was also a major obstacle to the completion of our experiments. Only after we actively blocked approaching predators from their intended prey were we able to complete the study.

This study supports the idea that predation-risk averse behavior has evolved in eusocial species with large colonies where predators are common. The results thus are comparable with predation-risk averse foraging

reported for ants (45,46). However, the ant and honeybee studies differed in design. Ant foragers chose among rewards differing between allopatric patches. On the other hand, honeybee foragers were presented with rewards differing among sympatric patches, suggesting that two levels of predation-risk averse foraging may exist in these large-colony eusocial species. Predation-risk sensitive foraging can be based on decisions at each foraging site, as we have shown for honeybees, and can be based upon recruitment to differing locations, as demonstrated using ants. A change from foraging to defensive behavior at a resource site may also occur (47). Even though eusocial organisms may have a buffer against the effects of predation, intense predation pressure produces risk-sensitive foraging decisions.

Acknowledgments

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