Response of Apis mellifera syriacaand A. m. armeniacatoNectar Variations: Implications for Agriculture

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Recommended Citation

Response of *Apis mellifera syriaca* and *A. m. armeniaca* to Nectar Variations: Implications for Agriculture

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Abstract: The foraging ecology of *Apis mellifera syriaca* and *A. m. armeniaca* was studied using artificial flower patches consisting of blue, white, and yellow flowers. Two experiments were performed with each race. Experiment I examined forager response to differences in sucrose reward molarity (quality of reward) associated with flower colors. Experiment II varied the quantity of sucrose reward associated with flower colors. *A. m. syriaca* and *A. m. armeniaca* each responded to quality and quantity differences between blue and white flowers. Prior studies show that *A. m. caucasica* and *A. m. ligustica* respond to reward quality difference, but they do not respond to reward quantity difference between blue and white flowers. However, all four subspecies partition foragers between yellow flowers, and the group consisting of blue-white flowers. The basic foraging differences of *Apis mellifera* subspecies may be useful for different agricultural pollination tasks to increase large scale crop productivity.

Apis mellifera syriaca ve *A. m. armeniaca*'nın Nektar
Değişkenliğine Reaksiyonu: Ziraat'deki Önemi

Özet: *Apis mellifera syriaca* ve *A. m. armeniaca* ırkı bal arılarının mavi, beyaz ve sarı yapay çiçek topluluğunda yayılma ekolojisi çalışılmıştır. Her bir ırk arı ile iki deney yapılmıştır. Birinci deneyde işçi arıların çiçek rengine göre değiştirilen sukroz konsantrasyon farklılığına ikinci deneyde ise sukrozun miktar değişikliğine nasıl bir reaksiyon gösterdikleri incelenmiştir. İki arı ırkı *A. m. syriaca* ve *A. m. armeniaca* sukroz konsantrasyon ve miktar değişikliğine mavi ve beyaz çiçekler üzerinde reaksiyon göstermiştir. Daha önceki çalışmalar beyaz ve mavi çiçekler üzerinde *A. m. caucasica* ve *A. m. ligustica*'nın konsantrasyon farklılığına reaksiyon gösterdiğini fakat sukroz miktarının değişkenliğine reaksiyon göstermediğini kaydetmiştir. Bu dört arı ırkında işçi arılar sarı ve mavi-beyaz olmak üzere çiçekleri paylaşarak işbölümü yapmışlardır. Bu işçi arıların çiçekler üzerinde gösterdiği yayılma taktikleri ziraat'de tozlaşma sayesinde üretimi artırmada büyük ölçüde katkıda bulunacaktır.

Introduction

Although honey bees have been observed pollinating agricultural crops for many centuries (See for review 1, 2, 3), only since the end of World War I have hives been actively managed in manners intended to increase fruit and seed production (4). Intensive honey bee pollination is essential in modern agricultural setting for high yields of fruits, nuts, and seeds for about 200 economically important crop plants (5, 6). The result of moving hives into agricultural fields for pollination has been astounding in terms of increased harvest. Consequently, demand has increased for honeybees as pollinators and secondarily for solitary bees as additional pollinators (4).

Of course, honey bees are not the only insect pollinator that are artificially managed. Leaf cutter bees (*Megachile rotundata*), alkali bees *(Nomia melanderi)*, several species of *Osmia,* and bumble bees (*Bombus* spp.) are managed in some areas for pollination of crops (7, 8, 9). However, honey bee use is usually far more economical since *Apis mellifera* colonies contain several thousand more foragers than those species and modern hives are easily transported from field to field (10). Honey bee value as a pollen vector is further increased because they often are effective pollinators of plant species which have coevolved with either birds or mammals (11). For the beekeepers, honey bees also provide an additional cash crop: honey. The vital role of honey bees and wild bees as pollinators which increase production and quality of crops in the European community (EC) has been reviewed and emphasized recently, Additionaly, by increasing seed set honey bee pollination has been proposed as a tool to control soil erosion (12, 13, 14).

Many crop species are either partially or totally self-incompatible and are dependent upon insects for pollen transfer among plants. Apple flowers seed set, for example, are 80-90 percent with pollen dispenser compared to 30 percent without pollen dispenser in

honey bee hives (15). Crops such as avocado (*Persea americana*) are protogynous dichogamous, requiring an insect pollen vector for any fruit set (16). However, modern agricultural practices, including the use of pesticides, usually decimate native and feral insect pollinator populations. Thus moving honey bees into fields for pollination is a critical factor for productivity.

Even self-compatible plants benefit from honey bee visitation. When autogamy is possible, two-thirds of the flowers visited by honey bees produce outcrossed seeds (17). Cross-pollination often produces increased crop quality and quantity. For example, cross-pollination increases blueberry (*Vaccinium conymbosum*) harvest 43 percent over-all and increases the early ripening crop by 140 percent (18). Similar results have been obtained with apricots (*Prunus armeniaca*), sunflowers (*Helianthus annuus*), loganberries (*Rubus loganobaccus*), lupins (*Lupinus albus*), and a host of other crop plants (19, 20, 21, 22). Furthermore, honey bee hives with their large numbers of foragers are often much more effective than native pollinators. For example, in a study of oil seed sunflower (*Helianthus annuus*), only 11 percent were pollinated by native bees while 83 percent were pollinated by honey bees (23).

Even though honey bees are crucial pollinators for modern agriculture, races of *Apis mellifera* typically used in the United States (*A. m. ligustica* and *A. m. carnica*) often fail to produce hybrid seeds between plant varieties. Inter-race plant hybrids are agriculturally important because they combine desirable characteristics, and often show "hybrid vigor" through production of larger fruit or bigger crops (9). This problem stems from the flower fidelity of honey bee foragers. Although all morphs of flowers at a location will typically be visited by bees from the same hive, even simultaneously visited, each bee will visit just one type of flower. A difference as simple as color variety is sufficient to isolate plants in terms of pollen flow (24, 25, 26, 27, 28). Attempts to produce hybrids between alfalfa clones using honey bees thus failed (29, 30). Similarly, production of hybrid cotton (*Gossypium* spp.) commercially has not been achieved even when planting alternating varieties by rows and columns, and still represents a major agricultural problem (31, 32).

In other cases, honey bees fail to facilitate hybrid seed production because they limit visitation to one flower variety, visiting different flower morphs at different times of the day (33). Attempts to produce hybrid kale (*Brassica oleraceae*) failed for this reason (34, 35, 36, 37). Even the use of hive bristles to increase pollen

exchange has not been effective in hybrid seed production (38).

Unfortunately, almost all of the data collected on honey bee foraging is based on studies using only the Italian race. Since behavioral differences exist among races in terms of hive defense and aggressiveness (39), behavioral differences are also likely to exist among races in foraging behavior. Flower fidelity of *A. m. ligustica* thus may not be representative of all *A. mellifera* races. Potentially, then, different races of *A. mellifera* might exist which would facilitate very different agricultural pollination tasks. Here we present experiments that examined flower choices of the native Anatolian honey bee subspecies *A. m. armeniaca* and *A. m. syriaca* when nectar rewards differed in quantity or quality among flower morphs.

Materials and Methods

Study sites: The same experiments were performed with each of the two races of *Apis mellifera* studied. Observations of *A. m. syriaca* were undertaken 10 km east of Şanlıurfa, Turkey (Syrian-Turkish inland border). Geographically, this region is part of the arid Harran Valley, which is characterized by long hot-dry summers and mild winters. Bees from an *A. m. syriaca* traditional mud hive were studied. The Syrian race is known as aggressive, with a specialized hive defense reaction against wasp predators (39).

The experiment was repeated using *A. m. armeniaca* in the mountains surrounding Kars, Turkey (Turkish border with Armenia). This region is known for its short, mild summers and long, snowy winters. Foragers from an *A. m. armeniaca* (39) eighteen frame hive were studied. Armenian honey bees are known as aggressive and nervous on the comb (40).

Artificial Flower Patches: All experiments were performed using artificial flower patches of the Wells *et al.* design (27, 28, 29) to control rewards associated with flower morphs. A flower was a 30 mm Plexiglass square, 4 mm thick, painted on the lower surface, and mounted on a 90 mm pedicel of 6 mm doweling. Each flower contained one 3 mm deep hole, 2 mm in diameter, located in a corner of the upper surface. The hole served as a nectary. Flower morphs differed solely in color, and were either blue, yellow, or white (Testor paint No. 1208, 1214, and 1245 respectively: see (29) for reflectance spectra). Flowers were spaced 75 mm apart in rows and columns of a Cartesian coordinate system. The three color morphs were always in equal number and randomly

arranged as to color in a flower patch (36 flowers: 12 yellow, 12 blue, 12 white). The flower-patch background color was brown. Flowers within a patch were arranged between sections, and periodically within sections, of an experiment so that flower position would not be a factor. Flowers were washed in unscented detergent solution, triple rinsed in tap water, and then air dried after each use.

Experimental Protocol: Bees at each study site were trained to visit a watch glass provisoned with 10 μL/L clove-scented 1M sucrose solution located at an experimental site 150 m from the hive. The watch glass was removed at the initiation of an experiment and replaced with an artificial flower patch provisioned with unscented sucrose solution.

Bees were allowed to freely choose which flowers to visit. Each bee visiting the flower patch was individually marked the first time it landed on a flower. The flowers visited by each bee were recorded. Bees used in an experiment were naive in that they had not previously visited an artificial flower patch. Unmarked bees were removed and caged during the experiment.

A new set of bees were used in each experiment. Two experiments were performed with both of the races of honey bees studied. Each experiment consisted of four sections performed sequentially and without interruption. Flowers were refilled as emptied with the same quantity of sucrose reward just consumed.

Experiment I - reward quality difference. Section 1: All flowers contained 5 μl unscented 1M sucrose solution (Experimentall control). **Section 2:** Blue flowers contained 5 μl 2M sucrose while white and yellow flowers contained 5 μl 1M sucrose reward. **Section 3:** White flowers contained 5 μl 2M sucrose while blue and yellow flowers contained 5 μl 1M sucrose reward. **Section 4:** Yellow flowers contained 5 μl 2M sucrose while blue and white flowers contained 5 μl 1M sucrose reward.

Experiment II - reward quantity difference. Section 1: All flowers contained 5 μl unscented 1M sucrose solution (Experimental control). **Section 2:** Blue flowers contained 2.5 μl 1M sucrose while white and yellow flowers contained 20 μl 1M sucrose reward. **Section 3:** White flowers contained 2.5 μl 1M sucrose while blue and yellow flowers contained 20 μl 1M sucrose reward. **Section 4:** Yellow flowers contained 2.5 μl 1M sucrose while blue and white flowers contained 20 μl 1M sucrose reward.

Data Analysis: Flower visitations of each bee were recorded. Differences in flower choice among bees by section were tested using a chi-square test of homogeneity (test #1H_0: Flower choice did not differ among bees). When significant differences existed among bees, foragers were partitioned into two groups based upon foraging behavior reported for *A. m. ligustica* (26, 27, 28, 41). Bees were divided into those who visited yellow first versus bees who first visited either blue or white (Section 1: first flower visited). Differences in flower choice between groups by section were tested using a chi-square test of homogeneity (test #2 H_0: Flower choice did not differ among groups). When significant difference existed among groups, average percent visititation to each flower color morph (among bee means and standard errors) in each section of an experiment were plotted. Then groups were analyzed separately for change in flower choice among sections using a chi-square test of homogeneity (test #3 H_0: Flower choice did not differ among sections within a group). Statistical tests and procedures are from (42) and (43).

Results

Reward quality difference: *Apis mellifera syriaca;* Flower choice differed within sections among bees (test #1: $X^2 > 846$, df=20, P<0.001 for each section; N=11 bees). Also, flower choice differed among groups within sections (test #2: $X^2 > 777$, df=2, P<0.001 for each section). Bees that first visited either blue or white flowers (N=8) visited few yellow flowers (2502 flowers visited, only 2 were yellow), while bees that first visited yellow flowers (N=3) rarely visited either blue or white flowers (Figure 1). Flower choice of the blue-white group bees differed among sections (test #3 limited to blue versus white flowers: X^2=291, df=3, P<0.001). Blue-white group bees preferred blue flowers in Section 2 and white flowers in Section 3, in each case the color containing the higher molar sucrose reward. No evidence existed that the yellow group bees changed frequency of visitation to yellow flowers among section (983 flowers visited, 4 were not yellow).

Apis mellifera armeniaca; Flower choice differed within sections among bees (test #1: $X^2 > 679$, df=34, P<0.001 for each section; N=18 bees). Furthermore, flower choice differed among groups within sections (test #2: $X^2 > 462$, df=2, P<0.001 for each section). Bees with fidelity to blue and white flowers (N=10) visited only 64 yellow flowers (1588 flowers visited). Of those 64 visits to yellow flowers, 63 were made by just two bees. Most bees that first visited yellow flowers rarely visited either blue or white flowers (7 bees visited
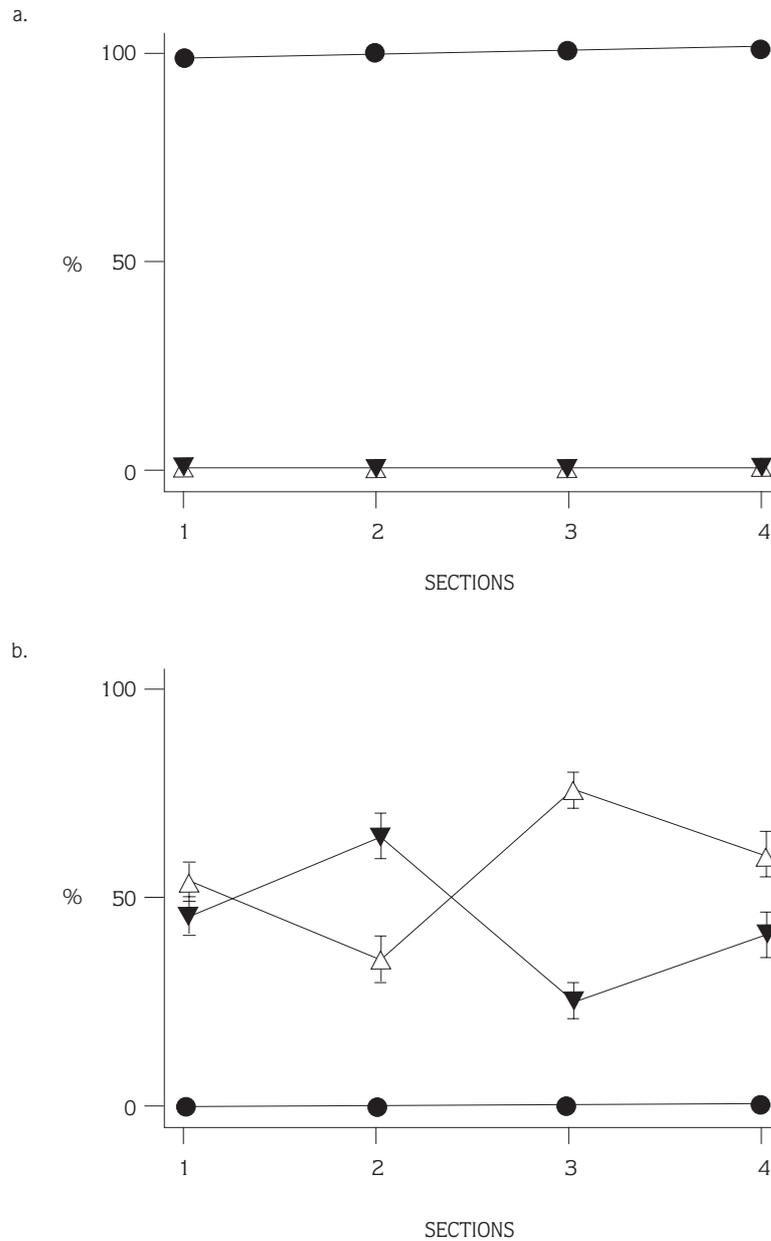
a.

b.

Figure 1.   *Apis mellifera syriaca* forager response to changes in sucrose reward molarity associated with flower color morphs (blue, white, & 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 (Figure 1a) and for bees first selecting etiher a blue or a white flower (Figure 1b). Reward molarities do not differ among flower color morphs in Section 1. Blue flowers offer a higher molar sucrose reward in Section 2, white flowers in Section 3, and yellow flowers in Section 4. Foragers respond to changes in sucrose reward molarity associated with blue and white flowers, but not yellow. Resource partitioning among sibling foragers was dominant to energy maximization-based foraging decisions.

1158 flowers, only 15 were not yellow). However, one bee that first visited yellow flowers then extensively visited both blue and white flowers in all four sections (168 flowers visited, 82 were not yellow). Flower choice of the blue-white group bees differed among sections (test #3 limited to blue versus white flowers: X^2=231, df=3, P<0.001). Blue-white group bees preferred blue flowers in Section 2 and white flowers in Section 3, in
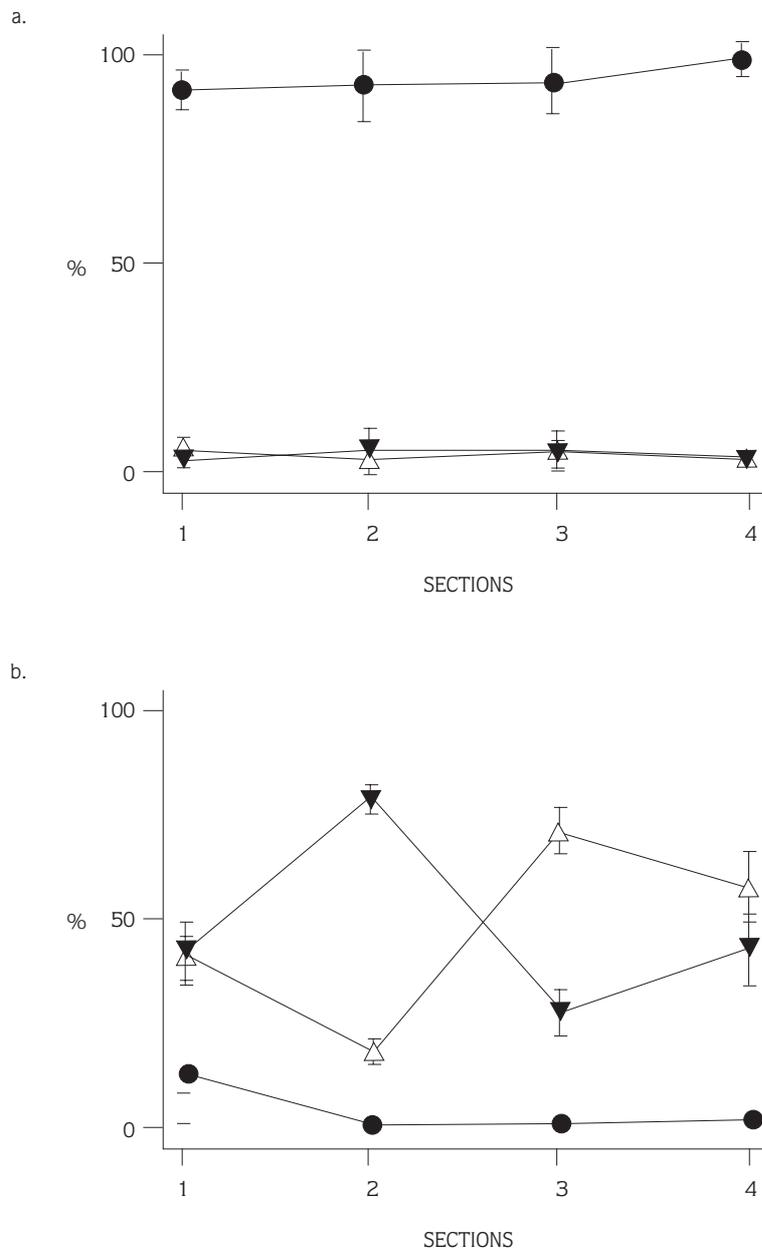
a.

SECTIONS

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Figure 2.   *Apis mellifera armeniaca* forager response to changes in sucrose reward molarity associated with flower color morphs (blue, white, & 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 (Figure 2a) and for bees first selecting etiher a blue or a white flower (Figure 2b). Reward molarities do not differ among flower color morphs in Section 1. Blue flowers offer a higher molar sucrose reward in Section 2, white flowers in Section 3, and yellow flowers in Section 4. Foragers respond to changes in sucrose reward molarity associated with blue and white flowers, but not yellow. Resource partitioning among sibling foragers was dominant to energy maximization-based foraging decisions.

each case the color containing the higher molar sucrose reward. No evidence existed that the yellow group bees changed frequency of visitation to yellow flowers among sections (Figure 2).

Reward quantity difference: *Apis mellifera syriaca;* Flower choice differed within sections among bees (test
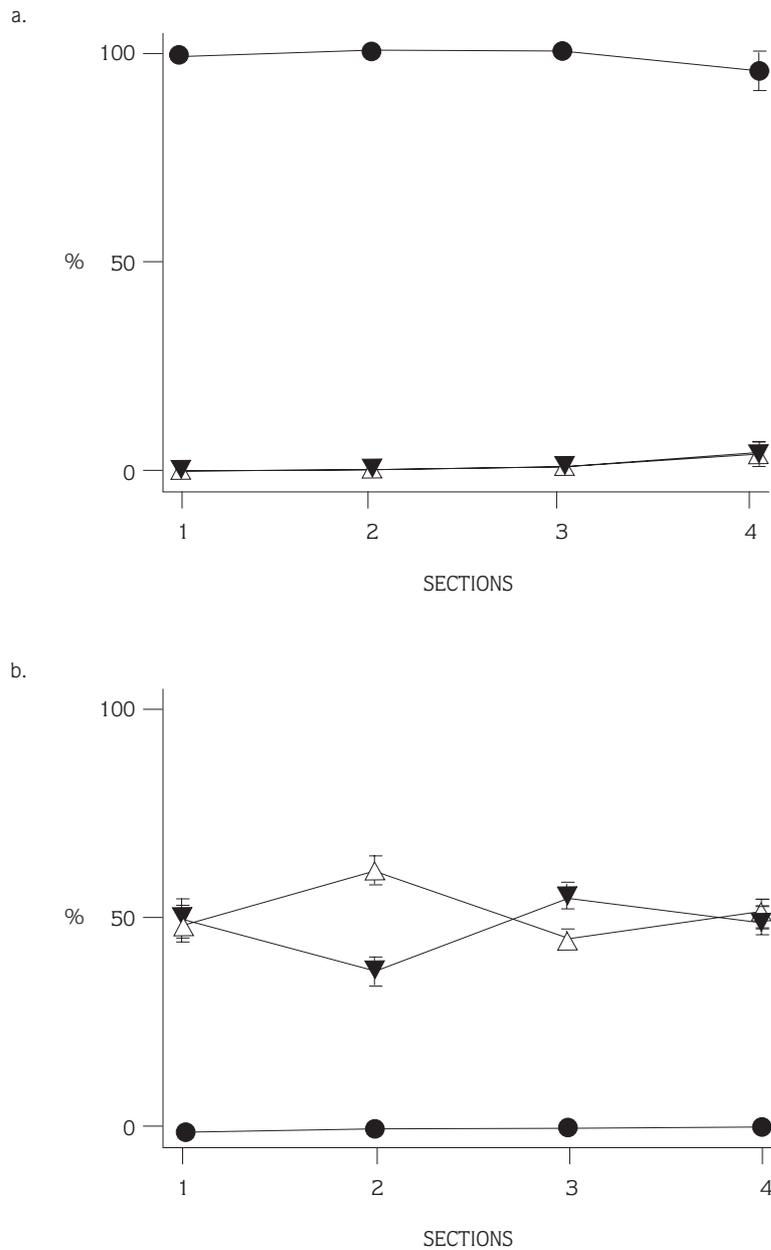
a.

b.

Figure 3.   *Apis mellifera syriaca* forager response to changes in sucrose reward quantity associated with flower color morphs (blue, white, & 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 (Figure 3a) and for bees first selecting either a blue or a white flower (Figure 3b). Reward quantities do not differ among flower color morphs in Section 1. Blue flowers offer a smaller quantity sucrose reward in Section 2, white flowers in Section 3, and yellow flowers in Section 4. Foragers respond to changes in sucrose reward quantity associated with blue and white flowers, but not yellow. Resource partitioning among sibling foragers was dominant to energy maximization-based foraging decisions.

#1: $X^2 > 915$, df=22, P<0.001 for each section; N=12 bees). Again, flower choice differed among groups within sections (test #2: $X^2 > 874$, df=2, P<0.001 for each section). Bees that first visited either blue or white flowers (N=8) rarely visited yellow flowers (2338 flowers visited, only 2 were yellow), and bees that first
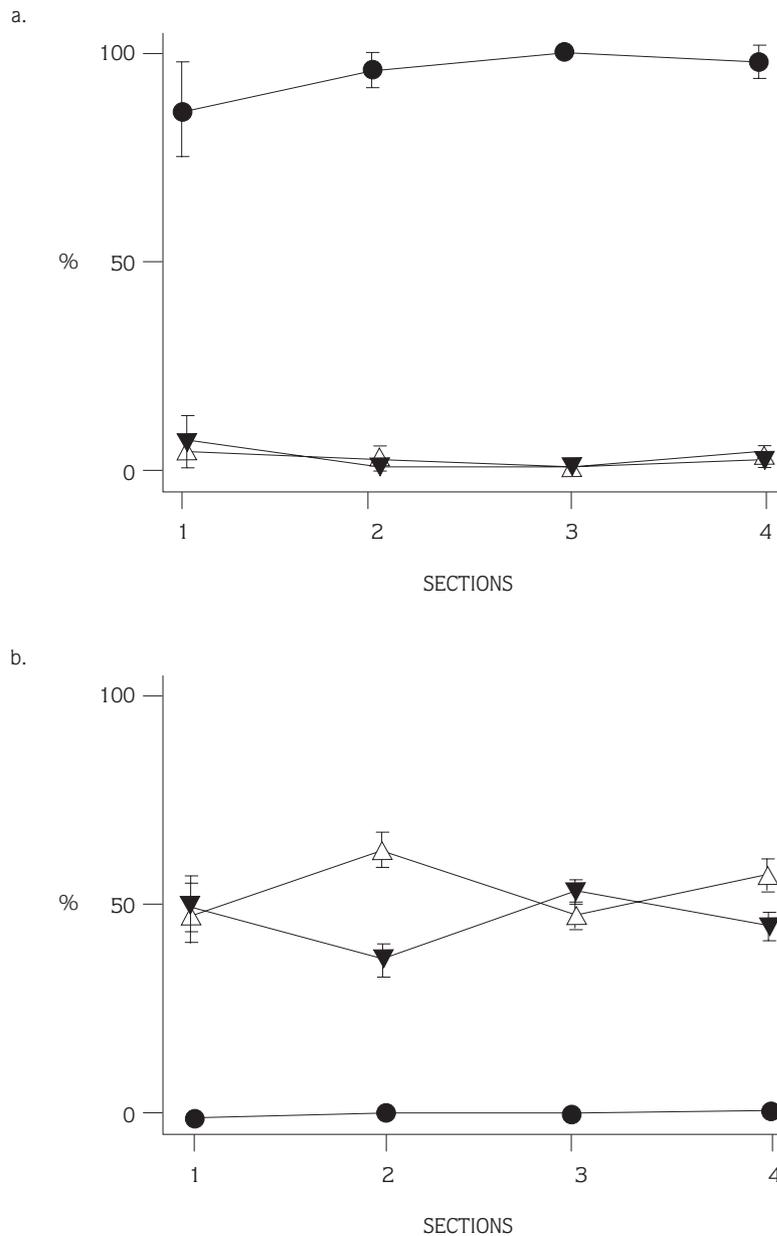
a.

b.

Figure 4.   *Apis mellifera armeniaca* forager response to changes in sucrose reward quantity associated with flower color morphs (blue, white, & 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 (Figure 4a) and for bees first selecting etiher a blue or a white flower (Figure 4b). Reward quantities do not differ among flower color morphs in Section 1. Blue flowers offer a smaller quantity sucrose reward in Section 2, white flowers in Section 3, and yellow flowers in Section 4. Foragers respond to changes in sucrose reward quantity associated with blue and white flowers, but not yellow. Resource partitioning among sibling foragers was dominant to energy maximization-based foraging decisions.

visited yellow flowers (N=4) visited few blue or white flowers (1373 flowers visited, 27 not yellow). Flower choice of the blue-white group bees differed among sections (test #3 limited to blue versus white flowers: X^2=28, df=3, P<0.001). Blue-white group bees showed a slight preference for white flowers in Section 2 and for blue flowers in Section 3, in each case the color containing the greater quantity reward. Also, flower

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choice differed among sections for the yellow group bees (test #3: $X^2=40$, df=6, P<0.001). Of the 27 flowers visited that were not yellow, 24 were in Section 4 where yellow flowers presented the smallest quantity reward of the three color morphs (Figure 3).

Apis mellifera armeniaca; Flower choice differed within sections among bees (test #1: $X^2>544$, df=26, P<0.001 for each section; N=14 bees). Furthermore, flower choice differed among groups within sections (test #2: $X^2>470$, df=2, P<0.001 for each section). Bees with fidelity to blue and white flowers (N=10) never visited a yellow flower (1304 flowers visited), while bees that first visited yellow flowers (N=6) visited few blue or white flowers (977 flowers visited, only 50 were not yellow). Flower choice of the blue-white group bees differed among sections (test #3: limited to blue versus white flowers: $X^2=17$, df=3, P<0.001). Blue-white group bees demonstrated a slight preference for white flowers in Section 2 and for blue flowers in Section 3, in each case the color containing the greater quantity reward (Figure 4). Difference in flower choice among sections for yellow group bees was due to one bee extensively sampling blue and white flowers in Section 1.

Discussion

A. m. armeniaca and *A. m. syriaca* responded similarly to differences in reward quality. In each experiment some foragers visited only yellow flowers while their siblings limited visitation to blue and white flowers (individual constancy). That division of foragers persisted, regardless of differences in molarity of rewards offered among flower color morphs. However, bees visiting blue and white flowers in both experiments preferred blue flowers over white when the blue morph offered the higher molar reward (Section 2), and preferred white over blue when white contained the higher molar reward (Section 3). When rewards did not differ between blue and white flowers in Section 1, bees limiting visitation to blue and white flowers showed no color preference as a group. Although no difference in reward existed between blue and white flowers in Section 4, bees continued to favor white flowers, probably because white contained the higher molar reward in section 3. Bees visiting yellow flowers did not switch to blue or white flowers in response to difference in reward (Sections 2 & 3), nor did blue-white bees switch to yellow flowers when the yellow morph contained the higher molar reward (Section 4).

Response of both Syrian and Armenian honey bees to difference in quantity of reward (Experiment II) was similar to that observed when molarity of reward diffeed

among flower color morphs. Some bees visited only yellow flowers while their siblings visited only blue and white flowers. Blue-white group bees preferred white flowers when the white morph contained the greater quantity reward, and increased vistation to blue flowers when the blue morph offered the greater quantity reward. However, response was not as strong as to reward quality difference.

Unlike experiments where reward quality was varied, *A. m. syriaca* showed a slight response to decreased quantity of reward offered by yellow flowers, increasing visitation to blue and white flowers from 0.3 to 6.0 percent (20 percent increase). On the other hand, *A. m. armeniaca* did not respond to a decrease in reward quantity offered by yellow flowers.

Flower fidelity of *A. m. armeniaca* and *A. m. syriaca* corresponds to reported behavior of both *A. m. ligustica* and *A. m. caucasica* when rewad molarity differs among blue, white, and yellow flower morphs (28, 44). Some bees visit only yellow flowers while their siblings restrict visitation to blue and white flowers. Bees visiting blue and white flowers will readily switch flower fidelity to blue or to white based on changes in molarity of rewards. However, bee visiting yellow flowers will not switch fidelity to blue or white flowers, and bees visiting blue and white flowers will not change fidelity to favor yellow, even when that means obtaining a lower caloric reward.

Behavior of *A. m. armeniaca* and *A. m. syriaca,* when presented differences in reward quantity among blue, white, and, yellow flowers, was similar to foraging of *A. m. ligustica* and *A. m. caucasica* in that bees partitioned the resource (28, 44). Some bees limited visitation to yellow flowers while siblings visited only blue and white flowers.

Unlike either *A. m. ligustica* or *A. m. caucasica, A. m. armeniaca* and *A. m. syriaca* respond to differences in reward quantity between blue and white flowers. *A. m. ligustica* and *A. m. caucasica* foragers visiting blue and white flowers do not show a preference for white flowers when white offers the greater quantity reward, nor do they favor blue flowers when blue offers the greater quantity reward (28, 44. That fundamental difference in behaviors may correspond to predation risk, since nonfrequently rewarding flowers increase a bee's exposure to visually hunting specialized predators such as the beewolf (*Philanthus triangulum,*) and bee predatory wasps (*Vespa orientalis* and *Vespa crabro*) (45). Specialized bee predators are quite prevalent in regions inhabited by the Syrian and Armenian races, but rare in areas where the Italian and Caucasian races originated

(39).

Variation in forager behavior correlated with *A. mellifera* subspecies present opportunities to develop different honey bee races for alternative specialized pollination tasks. For example, lineages of *A. m. syriaca* can be developed through breeding for use in hybrid seed production. Under intensive pollination schemes flower reward quantities are quickly depleted. A honey bee lineage whose foragers tend to abandon resource partitioning as reward quantities are depleted would increase pollen flow between plant varieties (*i.e.* a tendency in *A. m. syriaca* which could be further developed through selective breeding). On the other hand, resource partitioning by *A. m. ligustica* and *A. m. caucasica* could be used to minimize inter-specific plant pollination, which is particularly important when using inter-crop techniques instead of insectisides to control crop pests (insecticides reduce insect pollinator as well as insect pest populations and thus can reduce crop productivity: 46, 47).

Anatolia, with many different native subspecies of *A. mellifera*, is ideal for differential use of honey bee races in modern agriculture. Advantages of using a particular honey bee race may occur because it is adapted to the environment or because it reduces the movement of honey bees from region to region and thus will minimize honey bee disease spread (*e.g.* varroa mites). Recent data showing a genetic basis for worker task specialization within a hive (48, 49, 50), and the innate basis of both individual contancy and energy maximization foraging behaviors of honey bees (41), present hope that breeding programs may further select desirable foraging traits for specific agricultural pollination tasks (51).

The Southeast Anatolia Project (GAP) presents a perfect apportunity to combine biological and agricultural sciences to maximize productivity and quality of crop raised in Anatolia. Manipulation of both plant agricultural techniques and honey bee pollination methods can significantly increase crop productivity (52). The potential results are that economically important crops such as cotton may provide harvest that can be increased by 200 percent per acre by selecting cotton varieties and races of honey bees (53) for use in Southeast Anatolia.

Acknowledgments

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