

Article

Foraging Behavior of the Japanese Honeybee in an Artificial Condition

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Abstract

Flower choice of *Apis cerana japonica* was studied using color dimorphic artificial flower patches when reward differences were correlated with flower colors. Behavior of bees visiting flower patches containing blue and yellow flowers was compared to behavior on flower patches containing blue and white flowers. When presented blue-yellow dimorphic flower patches some bees visited only blue flowers while the remaining bees limited visitation to yellow flowers. That flower fidelity persisted in spite of reward quality, quantity, or frequency differences existing between flower colors (Individual Constancy Behavior). In contrast, bees visiting blue-white dimorphic flower patches each extensively visited both blue and white flowers when rewards did not differ between the two flower colors. However, bees limited visitation to the blue color morph when blue flowers offered a reward of higher quality than that offered by white flowers. Those bees would switch to white flowers when the white color morph contained the higher quality reward (Energy Maximization Behavior). Bees did not respond to reward quantity differences on blue-white dimorphic flower patches, nor was a consistent response to reward frequency differences observed on blue-white dimorphic flower patches. Foraging of the Japanese honeybees, *A. c. japonica*, was like that reported for European honeybees, *A. mellifera*, but different from that of Indian honeybees, *A. c. indica*.

Key Words: *Apis cerana japonica*, individual constancy behavior, energy maximization behavior, artificial flower patches

Honeybees have long been valued for the honey and beeswax they produce. Early domestication of European honeybees, *Apis mellifera*, and Asian honeybees, *A. cerana*, have enhanced honey and wax harvests (Joshi *et al.*, 1980; Crane, 1992). However, interest in honeybees as agricultural crop pollinators has occurred only within the last two centuries (Free, 1970). The role of honeybees as pollen vectors in modern agriculture now is far more valuable than are honey and wax crops (Free, 1970). Consequently, predicting the foraging actions of honeybees has become an important aspect of agricultural crop management.

The foraging behavior of *A. mellifera* is dominated by a peculiar type of flower fidelity known as individual constancy (Wells *et al.*, 1981, 1983). Each bee harvests from just one type of flower; it does so even when a choice of flower types exist at a foraging location. However, different foragers specialize on different flower morphs (Aristotle, c. 340 B.C.; Christy, 1883; Bennett, 1883; Grant, 1950; Free, 1966; Moezel *et al.*, 1987). What makes that behavior peculiar is that flower fidelity persists in spite of flower variety-related differences in nectar quality (sugar molarity) or quantity (Wells and Wells, 1983). Further, flower fidelity of bees is not affected by differences in reward frequencies among flower varieties (Wells and Wells, 1983, 1986). Apparently, individual constancy behavior is neither driven by

recognized energetic considerations nor is it risk averse.

Even though basic *A. mellifera* forager action is characterized by individual constancy, within certain subgroups of flower-types foraging may be defined by energy maximization criteria (Wells and Wells, 1986; Wells *et al.*, 1992). For example, when artificial flower patches contain blue, white, and yellow flowers, some foragers will visit only yellow flowers. Other foragers will visit both blue flowers and white flowers, but not yellow flowers. When blue flowers have the greater caloric reward, bees visiting both blue and white flowers will limit their visitation to blue flowers and no longer visit white flowers. However, bees visiting yellow flowers will not switch fidelity, nor will bees visiting both blue and white flowers visit yellow flowers when the yellow flower morph contains the calorically superior reward (Wells and Wells, 1986; Wells *et al.*, 1992). Thus, honeybees have a hierarchy of foraging behaviors dominated by individual constancy. Those experiments also demonstrate that individual constancy is not the result of forager memory limitations. Comparison of *A. m. ligustica* (Italian race of the European honeybee) to *A. c. indica* (the Indian honeybee) flower choice in flower patches brought a new perspective to our model of honeybee foraging. Foraging of *A. m. ligustica* is dominated by individual constancy while *A. c. indica* foraging is totally based upon energy maximization (Wells

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and Rathore, 1994). That difference in behavior rules out the possibility that individual constancy is the product of domestication or honeybee social structure. However, behavior may be species defined (for a variety of reasons). Alternatively, the different environments (tropics vs temperate) of these two taxa may select for different behaviors. Presented are data on the foraging behavior of *A. c. japonica* when flower color choices exist in a flower patch. Experiments are designed to test whether forager behavior is species defined or is the product of foraging environments. The experiments may also yield data useful for selection of *Apis* species and races with behaviors amenable to specific agricultural pollination tasks.

Materials and Methods

Experiments were performed using the Japanese honeybee, *Apis cerana japonica*, foraging on artificial flower patches. The Japanese honeybee is an ecotype of *A. cerana* (the Asian honeybee) which occurs throughout Japan except Hokkaido.

Artificial flower patch design

All experiments were performed using artificial flower patches containing 36 flowers. Artificial flower patches were used to control flower morphologies, flower morph distribution and abundance, and nectar rewards. Flower patches and flowers were of the Wells design (Wells *et al.*, 1981, 1983, 1992). Flowers were 30 × 30mm Plexiglass (acrylic plastic) squares 4mm thick, each mounted on a 90mm pedicel of 6mm doweling. Flowers each contained one nectary consisting of a 3mm deep hole, 2mm in diameter, located in a corner on the upper surface. Flower morphs differed solely in color. A flower was painted blue, yellow, or white on the lower surface (Testor paint No.1208, 1214 and 1245 respectively). Flowers were spaced 75mm apart in rows and columns of a Cartesian coordinate system. The background for flowers was brown (Krylon brand paint No.2506).

Experimental design

The artificial flower patch presented bees is made of 18 blue and 18 yellow flowers (Expt. 1, 3 and 5) or 18 blue and 18 white flowers (Expt. 2, 4 and 6). Those 2 color dimorphisms have been used in experiments with both *A. mellifera* and *A. c. indica*, so results are directly comparable (Wells and Wells, 1986; Wells *et al.*, 1992; Wells and Rathore, 1994). The 2 flower color morphs in a patch were always equal in number and randomly placed with respect to color on the Cartesian grid, with grids in each section of an experiment periodically changed so that flower position would not become a factor. Flowers were washed in unscented detergent solution, rinsed in tap water, and air dried after each use. All experiments were performed in Uji City, a suburb

of Kyoto (Japan), using a hive belonging to a Japanese beekeeper (Mr. K. Noguchi).

An experiment was initiated by training a new set of bees from an 8-frame hive to fly 60m to a clear watch-glass containing clove scented 1M sucrose following previously published methods (Johnson and Wenner, 1970; Wells *et al.*, 1981). Each experiment used a different set of bees, 10 individually marked bees per experiment. The watch-glass was removed, replaced with a color dimorphic flower patch provisioned with 5 μ l of 1M unscented sucrose in each flower of both color morphs, and foragers allowed to freely choose which flowers to visit.

Experiments each consisted of 3 sections performed sequentially without interruption. Flowers of both colors in Section I of every experiment contained 5 μ l of 1M unscented sucrose solution. Sections II and III utilized the same flower dimorphism, volume of reward, and foragers as section I of an experiment; however, rewards in the two flower morphs differed in sucrose molarity (quality), quantity of reward per flower, or frequency of flowers offering reward. The same rewards presented in Section II were used in Section III of an experiment, but were reversed as to association with flower morph. Nectaries were refilled with their designated reward in each section as they were emptied. All experiments were performed outdoors.

Experiments 1 (blue-yellow) and 2 (blue-white) used a reward difference of 5 μ l-1M versus 5 μ l-2M sucrose in Sections II and III. Experiments 3 (blue-yellow) and 4 (blue-white) used a reward difference of 2.5 μ l-1M versus 20 μ l-1M sucrose in Sections II and III. Experiments 5 (blue-yellow) and 6 (blue-white) used a reward frequency difference of 1/3 of the flowers offering a 5 μ l-1M sucrose reward (2/3 empty) versus all flowers of the alternative color morph offering a 5 μ l-1M sucrose reward in Sections II and III.

Flower visitation of each bee was recorded. Average percent visitation to blue flowers (among bees) in each section of an experiment was analyzed for statistical deviation from the result expected if bees were to indiscriminately visit flowers with respect to color (50% blue visitation) using a *t*-test (Bailey, 1975).

Foraging model predictions of flower choice

The behavior of *A. c. japonica*, under the 'energy maximization' hypothesis (calories/time), should result in forager constancy to the flower morph which yields the greater net caloric reward when a difference exists (*e.g.* 1M vs 2M sucrose). If a worker is foraging on the flower morph with the lower molarity, lower quantity, or less frequent reward it is expected to switch to the morph offering the higher net caloric reward. When flower morphs hold equivalent caloric rewards (Section I), both flower morphs should be visited extensively by the population of foragers (Wells and Wells, 1986).

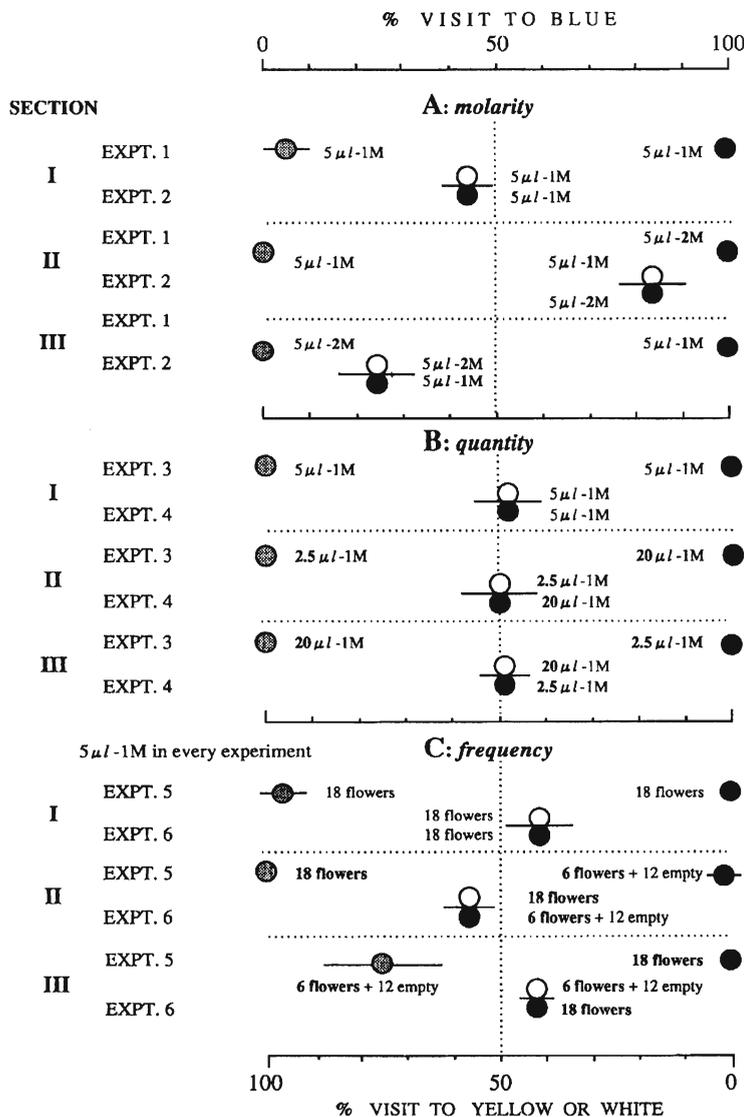


Fig. 1. Results of all experiments. Experiments 1, 3 and 5 presented bees 18 blue and 18 yellow flowers, while Experiments 2, 4 and 6 presented bees 18 blue and 18 white flowers. Section I offered bees 5 μ l-1M sucrose in both flower colors (all experiments have the same condition). Section II of part A (reward molarity difference) offered bees 5 μ l-2M sucrose in blue flowers and 5 μ l-1M sucrose in the alternative flower color; Section II of part B (reward quality difference) 20 μ l-1M sucrose in blue flowers and 2.5 μ l-1M sucrose in the alternative flower color; and Section II of part C (reward frequency difference) a 5 μ l-1M sucrose in only 1/3 of the blue flowers (2/3 had no reward) and a 5 μ l-1M sucrose in all flowers of the alternative color morph. Section III was reversed experiments to Section II. Ten bees were used in each experiment. Bees in Experiments 1, 3 and 5 fell into 2 distinct behavioral groups; those limiting visitation to blue flowers (black circles; $n = 5$ in A and C; $n = 6$ in B) and those visiting exclusively yellow flowers (dotted circles; $n = 5$ in A and C; $n = 4$ in B). Foragers in Experiments 2, 4 and 6 behaviorally acted as a single group (white-and-black circles; $n = 10$). The center of circles represent mean percent visitation to blue flowers (toward right) or to yellow or white flowers (toward left), and short lines with circles the standard error of the mean.

Conversely, behavior in all experiments should be identical, according to the 'individual constancy' model, with some foragers constant to each flower morph regardless of reward or reward difference between flower morphs (Wells and Wells, 1983).

All foragers, according to the 'innate constancy' model, should limit visitation to only one of the flower colors in an experiment, but unlike constancy resulting from energy maximization, not based on net caloric yield (Grant, 1950).

Under the conditions presented the 'risk aversion' model predicts that bees will limit flower visitation (Expt. 5 and 6) to the color morph most frequently offering a reward (Real, 1991). When reward frequency does not differ between flower morphs, the risk aversion model does not predict that either flower morph should be favored, or that a change in behavior will be observed (Expt. 1-4).

Foragers, according to the 'memory limitation' hypothesis, should not be able to switch fidelity to the flower morph

offering the greater net caloric reward or most frequent reward in either blue-yellow or blue-white flower patches (Waser, 1986).

Comparative behavior predictions of forager flower choice

If behavior is species defined, then foraging of *A. c. japonica* is expected to be similar to that of *A. c. indica*. Thus, foraging should be predicted by the energy maximization model on both blue-yellow and blue-white dimorphic flower patches.

Results

Differences in reward quality

Results present in Fig. 1A. When presented blue-yellow dimorphic flower patches where reward quality was varied

between flower colors (Expt. 1), bees 1 through 5 limited visitation to yellow flowers while bees 6 through 10 visited exclusively blue flowers. Flower fidelity of each bee remained unchanged throughout the experiment even though blue flowers offered the higher molarity reward in Section II, and yellow flowers the higher molarity reward in Section III. Neither group of bees chose flowers randomly with respect to color in any section of the experiment (For each section: $t > 19.3$, $df = 4$, $p < 0.001$), nor did either group change behavior in response to changes in rewards offered by each color morph. In contrast, when offered blue-white dimorphic flower patches where reward quality was varied between flower colors (Expt. 2), each bee extensively visited both blue and white flowers when both flower color morphs contained 1M sucrose reward (Section I: $t = 1.14$, $df = 9$, $p > 0.20$). However, when blue flowers contained the higher molar reward, those bees limited visitation to blue flowers (Section II: $t = 7.12$, $df = 9$, $p < 0.001$). Next, when white flowers contained the higher molar sucrose reward, those bees limited visitation to white flowers (Section III: $t = 3.86$, $df = 9$, $p < 0.01$).

Differences in reward quantity

Results present in Fig. 1B. Experiment 3 also presented foragers blue-yellow dimorphic flower patches, however, reward quantity rather than quality was varied between flower colors. Bees 1 through 6 limited visitation to blue flowers while bees 7 through 10 visited only yellow in each section. Flower fidelity of each group persisted despite differences in reward quantity offered by blue and yellow flowers in Sections II and III ($t > 5.54$, $df < 4$, $p < 0.001$). Results correspond closely to those observed in Experiment 1.

Although bees in Experiment 4 were offered blue-white dimorphic flower patches, behavior did not change between sections as it had in Experiment 2. Each bee in all 3 sections

extensively visited both blue and white flowers ($t < 0.25$, $df = 9$, $p > 0.20$). Bees did not show a preference for blue flowers in Section II where blue flowers offered the greater quantity of reward, nor did they limit visitation to white flowers in Section III where white flowers contained the greater quantity of reward.

Differences in reward frequency

Results present in Fig. 1C. Behavior of bees in Experiment 5 was similar to that observed in Experiments 1 and 3. Bees were presented blue-yellow dimorphic flower patches where reward frequency was varied between flower colors. Bees 1 through 5 limited visitation to blue flowers while bees 6 through 10 limited visitation to yellow flowers. Flower fidelity of bees was not affected by changes in frequency of reward offered by the competing flower morphs ($t > 2.87$, $df = 4$, $p < 0.05$).

Bees in the corresponding experiment with blue-white dimorphic flower patches (Expt. 6) each extensively visited both blue and white flowers in all 3 sections. Foragers did not demonstrate a preference for either flower color in Section I ($t = 1.21$, $df = 9$, $p > 0.20$) or II ($t = 1.52$, $df = 9$, $p > 0.10$), but did show a statistical flower color preference (60% visitation to blue flowers) in Section III ($t = 3.31$, $df = 9$, $p < 0.01$). Since reward frequency differed between blue and white flowers in both Sections II and III, and bees responded minimally even in Section III to the reward frequency difference, it is doubtful that foragers generally react to reward frequency differences of the magnitude presented (33% vs 100% rewarding).

Individual constancy and energy maximization

Foragers in each experiment with blue-yellow dimorphic flower patches exhibited individual constancy. Bees visiting yellow flowers did not visit blue flowers and foragers

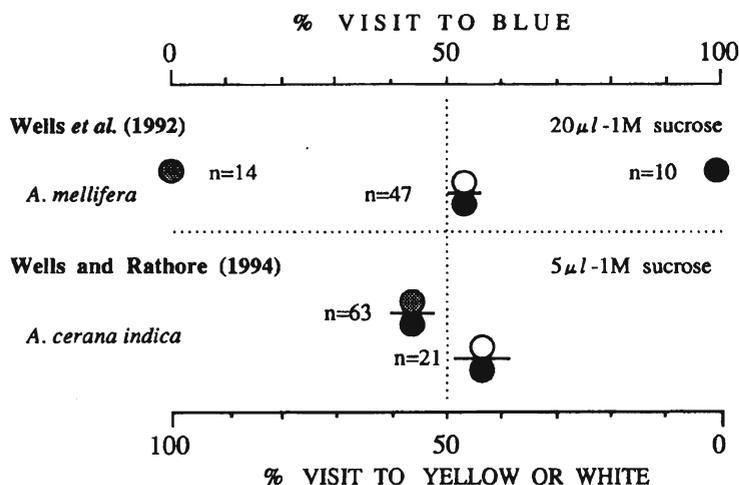


Fig. 2. Results of 2 published experiments for comparison with Fig. 1. The upper side of the figure is made from a part of Wells et al. (1992)'s data. *Apis mellifera ligustica* workers were presented 18 blue and 18 yellow or white flowers, each of which was filled with 20 μl-1M sucrose. The lower side is a part of Wells and Rathore (1994)'s data. The same flower patch was presented to *Apis cerana indica* workers. Each flower was filled with 5 μl-1M sucrose. Black circles indicate experiments on blue flowers; dotted circles on yellow flowers; white circles on white flowers. The mean percent visitation and its standard error is represented as Fig. 1.

visiting blue flowers did not visit yellow flowers. That dichotomy of foragers persisted regardless of differences in reward quality, quantity, or frequency. Further, bees rarely sampled the alternative flower morph. The 14 foragers constant to yellow sampled only 146 blue flowers while visiting 3568 yellow flowers. Conversely, the 16 foragers constant to blue flowers sampled only 29 yellow flowers while visiting 4586 blue flowers. When a bee did sample the alternative flower color, its preference was not changed—even when the reward was calorically superior in the alternative color morph.

In contrast, each bee foraging on blue-white dimorphic flower patches extensively visited both blue and white flowers when rewards were identical in the 2 color morphs (Section I of Expt. 2, 4 and 6). However, foragers limited visitation to the flower color offering the higher molarity reward when a difference in reward quality existed between blue and white flowers. That behavior was consistent with energy maximization considerations. Yet, bees failed to respond to reward quantity differences between blue and white flowers; instead they visited the 2 color morphs randomly. Forager response was not consistent when reward frequency differences existed on blue-white dimorphic flower patches.

Discussion

Fig. 2 shows the published data of *A. m. ligustica* and *A. c. indica* that corresponds to the Section I of Fig. 1. The behavior of *A. m. ligustica* was dominated by individual constancy, but individual-based energy maximization occurred within sub-groups of flowers when nectar quality differences exist (Wells and Wells, 1983, 1986; Wells *et al.*, 1992; see Fig. 2 upper). Foragers of *A. c. indica* in contrast did not exhibit individual constancy based flower fidelity. Rather, *A. c. indica* foragers limited flower visitation to the morph offering the higher quality reward even when presented blue-yellow dimorphic flower patches (Wells and Rathore, 1994; see Fig. 2 lower). The result of the present experiment was particularly interesting because foraging of *A. c. japonica* corresponded to that reported for *A. m. ligustica* rather than *A. c. indica*. Foragers of *A. c. japonica* in each experiment with blue-yellow dimorphic flower patches exhibited individual constancy, but did not in the blue-white experiments. Thus, *Apis* foraging behavior is not species defined. Instead, foraging appears to be governed by ecotype.

Knowing the reaction of *A. mellifera* and *A. cerana* subspecies to flower variability at a foraging site can be used to solve some agricultural crop pollination problems, particularly when special plant breeding goals exist, including the regulation of hybrid seed production. For example, Hanson *et al.* (1964) could have used *A. c. indica* rather than *A. m. ligustica*, or had they chosen alfalfa varieties not having flower differences, the problem reported in obtaining hybrid seed would not have occurred. Similar problems in produc-

ing hybrid seed have occurred in crops as diverse as crab-apple and Brussels-sprout (Boren, *et al.*, 1962; Johnson and Morgan, 1970; Faulkner, 1971, 1974; Free and Williams, 1973, 1983). Unfortunately, the data required to make those decisions did not exist at the time their experiments were performed. In that light, recognition of *Apis* taxa that have unusual foraging behaviors is worthy of immediate attention since several ecotypes of *A. cerana* are now threatened with extinction by the expanding use of *A. mellifera* for honey production (Ruttner, 1988; Verma, 1992). While those *A. cerana* subspecies threatened are not the best honey producers, they may have a far greater agricultural value as specialized pollen vectors, and thus be worthy of immediate conservation efforts.

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