

FORAGING CHOICES OF BUMBLEBEES ON EQUALLY REWARDING ARTIFICIAL FLOWERS OF DIFFERENT COLORS

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ABSTRACT

Laboratory-reared bumblebees were allowed to forage on 30 artificial flowers which were identical in morphology and reward schedule, but were marked by either a human-blue, a human-green, or a human-white landing surface. The probability of nectar rewards in the artificial flowers, and their spatial distribution, were manipulated experimentally. The bees' color choices in the different experimental treatments were compared.

The proportions of visits to the three colors deviated significantly from the expected random choice (1/3, 1/3, 1/3) for more than 50% of the bees. Of these bees, 38%, 32%, and 30% formed a preference for human-blue, human-green, and human-white, respectively. The frequency of nonrandom color choice, and the strength of the deviation from random choice, were highest when the different colors were placed in separate clusters, lower when they were placed in adjacent clusters, and lowest when they were randomly intermingled. Nonrandom color choice was also more pronounced when the bees were rewarded according to a constant schedule, rather than probabilistically. A statistically significant preference for human-blue was found during the bees' first three visits. The bees' tendency for "runs" of consecutive visits to the same flower color can partially account for their non-random color choices. Effects of innate preferences, early learning, generalization, and search-image formation on color choice are discussed.

INTRODUCTION

Bees and other pollinators with color vision readily learn to associate food sources with a specific color in classical conditioning experiments (Menzel et al., 1993). That is, they are able to use a color as a signal for an expected food reward. Bees are also able to learn several colors simultaneously as food signals (Menzel, 1969; Greggers and Menzel, 1993). This ability seems to be adaptive in many cases, since the differences in flower color between plant species are often accompanied by differences in nectar and pollen rewards (Proctor and Yeo, 1973; Faegri and van der Pijl, 1979). Additionally, changes in the production of reward over the lifetime of a single flower are often accompanied by changes in flower color (Weiss, 1995). Thus, the ability to associate flower color with reward probably helps

bees to form foraging preferences for certain flower species or certain flowering stages within a species (Menzel and Shmida, 1993).

But flower color is not always a reliable signal of reward. In plant species which are polymorphic for flower color, but not for floral morphology and reward, color is not correlated with profitability. In these cases pollinators are expected to maximize their foraging efficiency by foraging indiscriminately with respect to color. Such indiscriminate foraging has been recorded in some field studies on color-polymorphic flowers, but not in others. Levin and Watkins (1984) found a similar pollination frequency for two color-morphs of *Phlox drummondii* which were grown together in equal proportions. Wolfe (1993) did not find color-preferences in honeybees which pollinated human-white and human-

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blue *Hydrophyllum appendiculatum*. On the other hand, Kay (1976) and Stanton et al. (1989) found a marked preference of *Pieris* butterflies and *Eristalis* flies for human-yellow flowers over human-white flowers in wild radish (*Raphanus raphanistrum* L.). Waser and Price (1983) showed that bumblebees and hummingbirds prefer the human-blue morph of *Dephynium nelsonii* to the human-white morph. Scora (1964) reports a similar discrimination against unspotted mutants of *Monarda punctata* by bees and wasps. The previous foraging experience of the pollinators and the distributions of reward in the different colors were unknown in these studies.

A few laboratory studies, which investigated the choice behavior of bees on differentially-colored artificial flowers, report a variety of results as well. Waddington and Holden (1979) and Giurfa and Núñez (1989) observed the foraging choices of honeybees, which foraged singly in a laboratory patch of artificial flowers with two colors and equal rewards. The bees visited the two colors with similar frequencies, although considerable individual variation in behavior was observed in one study (Waddington and Holden, 1979). Wells and Wells (1983) carried out a similar experiment on four honeybees, and found that two of the bees foraged exclusively on human-yellow flowers, while the other two visited only human-blue flowers. Banschbach (1994), on the other hand, found a preference for human-blue in binary-choice experiments with equally rewarding human-blue and human-yellow flowers. The color choices of honeybees in other binary-choice tests with artificial flowers depended on the spatial arrangement of the flowers (Marden and Waddington, 1981). The previous foraging history of these bees were unknown in these studies as well.

In the present work we aimed to study the choices of naive pollinators in color-polymorphic situations. For this purpose we worked with naive bumblebees, and trained them simultaneously to several colors according to their own choice. After pretraining with a human-grey feeder, we recorded the foraging choices of bees in an array of artificial flowers which were identical in morphology and reward schedule, but were assigned to three different color displays. Since all colors were equally rewarded, our null hypothesis was that bees would forage randomly with respect to flower color because their foraging experience would lead to the formation of equal color-reward associations. This expectation may not be realistic because it does not take into account that a single visit to a feeder can change the choice behavior for all subsequent visits (Menzel, 1968). Additionally, pretraining with feeders that are uncolored to the human eye may also affect the subse-

quent color choices measured during the foraging session (Giurfa, 1991; Giurfa et al., 1995). In particular, bees are able to generalize the color information of such "neutral" feeders to the more perceptually similar colors offered during the foraging tests. However, our null hypothesis is valid in the sense that it provides a first-level, simple hypothesis that can be rejected or not. Our hypothesis thus constitutes a necessary first step towards testing more sophisticated and accurate hypotheses. We also considered the two following alternative hypotheses:

- A. The bees' foraging choices may be affected by innate color preferences. Under this hypothesis (the innate-attraction hypothesis) we expected all of the bees to choose preferably the same flower color in their very first foraging visits. In particular, we anticipated an affinity to human-blue, which has been reported in a few previous studies (Giurfa et al., 1995; see Lunau and Maier, 1995 for a review of earlier studies). Moreover, Menzel (1968, 1985) demonstrated a higher preparedness in honeybees to learn blue as a food-signal, in comparison with other colors. We also predicted that the preferred color morph will be chosen more often than other colors when the bees' complete foraging sequence is considered since they would stick to it after learning in their first visits that it provides reward.
- B. The bees' foraging choices may be affected by a difficulty to search efficiently for more than one floral display (Waser, 1986; Dukas and Ellner, 1993; Dukas and Real, 1993; Chittka et al., in press). Shifts among flower types are associated with longer flight durations than movements among flowers of the same type (Greggers and Menzel, 1993; Chittka et al., in press). Such long flight durations can be interpreted as memory constraints, which cause bees to work more slowly when switching between flower species. This memory constraint may also cause the bees to forage predominantly on one color, namely the color which they started to visit at the beginning of the foraging session. According to this hypothesis (the searching-efficiency hypothesis) we expected differences in color preferences among individual bees, which may be related to differences in their foraging histories.

A second aim of our experiments was to test how the spatio-temporal properties of the flowers of different colors affect the bees' choice behavior. For this purpose we recorded the bees' color choices for three patterns of spatial distribution of the artificial flowers, and for three reward schedules.

METHODS

Experiments were carried out in a 3×4 m flight room. Temperature ranged from 26 to 30 °C and relative humidity from 40 to 70%. The room was illuminated from 0630 to 1830 with 6 fluorescent light tubes. Observations were conducted during November 1994 and June 1995, between 0800 and 1630.

Colonies of naive *Bombus terrestris* (L.) were obtained from Kibbutz Yad-Mordechai, Israel. A total of 101 bees from five colonies were used for the experiments. All individuals in the colony were marked within 3 days of emergence. Pollen was supplied without restriction, directly to the hive. The bees were allowed to fly freely in the room between observation sessions. The bees were allowed to feed *ad libitum* from a human-grey nectar feeder for 2–3 h after each observation session. Then the feeder was removed and the bees were starved until the next observation session, on the following morning. "Neutral" colors such as human-grey can affect later color choices (Giurfa et al., 1995), because bees learn them and afterwards generalize to the most similar color signal (Giurfa, 1991). We tried to reduce

the impact of such generalization phenomena by using a pre-training feeder that also differed in size and structure from the artificial flowers presented in the tests. Moreover, we used (whenever possible) only black, white, or grey equipment between observation sessions to minimize uncontrolled color experience.

ARTIFICIAL FLOWERS

Thirty morphologically identical artificial flowers were used for experiments. The flowers were tube-shaped and 10 cm tall. Each flower was placed above a $10 \times 10 \times 8$ cm box which contained its electronic parts. A removable round plastic landing surface of 3.7 cm diameter was placed on top of each flower. This landing surface was colored either human-blue (10 flowers), human-green (10 flowers), or human-white (10 flowers). These colors correspond to blue, green, and blue-green, respectively, in the color vision system of bees (Menzel and Shmida, 1993; Chittka et al., 1994). The bee-color names will therefore be used from this point on. The flowers were placed on a 1.40×2.40 m hardwood table which was subdivided by a 6×20 position grid. The loci of the flower colors in a physiological chromaticity diagram, based on honeybee receptor curves, are shown in Fig. 1. Although we performed our experiments with bumblebees, honeybee receptor curves were used for color evaluation because the set of photoreceptors of most hymenoptera (including bumblebees) is very similar to that of the honeybee (Chittka et al., 1992; Peitsch et al., 1992). For the calculation of color loci, a D-65 norm-day light function and the hardwood table as adaptation background were also used. The flowers were either empty, or contained ca. 1 μ l 30% sucrose solution, according to experimental design. The spatial arrangement of the flowers depended on experimental treatment (Table 1, Fig. 2). An identical arrangement was used for all of the bees within one treatment. Between observation sessions, the landing surfaces were covered and were thus invisible and inaccessible to the bees.

At the end of a foraging visit to an artificial flower it was either refilled automatically or left empty, according to a predetermined reward schedule. Flower refilling

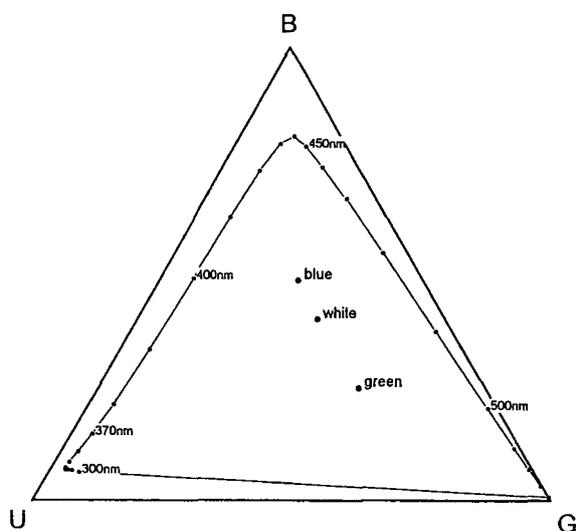


Fig. 1. A physiological chromaticity diagram for the colors which were used for the artificial flowers.

Table 1
Experimental treatments

Treatment	No. of bees	Spatial arrangement of color morphs	Flower refilling probability
Separate clusters	20	Separate	1
Adjacent clusters	19	Adjacent	1
Intermingled	22	Intermingled	1
Frequent refilling	19	Separate	1/2
Infrequent refilling	21	Separate	1/3

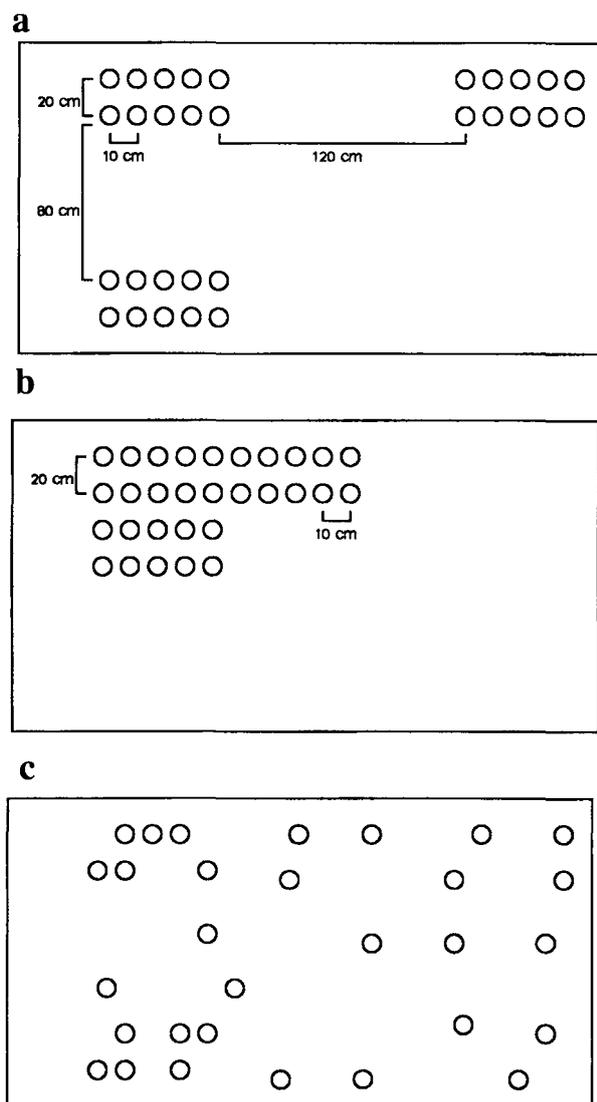


Fig. 2. The spatial arrangement of the flowers in the clustered (a), adjacent (b), and intermingled (c) treatments. In the clustered and adjacent treatments, the three flower colors were assigned randomly to the flowers, separately for each bee. In the intermingled treatment the same random assignment of colors was used for all bees. The bee colony was located at the other end of the flight room, ca. 2.5 m away from the flowers.

took place 2 s after the forager's departure, and did not interfere with the bees' activity. To prevent orientation by means of scent, we changed the colored plastic disks which served as landing surfaces before another individual was allowed to approach the artificial flowers.

EXPERIMENTAL DESIGN

We recorded the flower choices of naive untrained

workers, which foraged singly on the array of artificial flowers. Other individuals which approached the floral array were caught and caged until the end of the observation session. Each artificial flower was equipped with a photodetector, which was activated when the foraging bee inserted its head into the flower. The photodetector signals corresponded to flower visits, and were automatically recorded into a computer file. Data from the bees' first 150 flower visits were used for analysis.

Five experimental treatments were employed, as detailed in Table 1. In the first three treatments the independent variable was the spatial arrangement of the flowers (Fig. 2). In the separate-cluster, frequent-refilling, and infrequent-refilling treatments, we manipulated the refilling frequency of the flowers. In the separate-cluster treatment, each flower was refilled after it had been visited. In the frequent-refilling treatment, the flowers of all three colors were also full at the onset of each experiment (i.e., offered ca. 1 μ l of nectar), and were refilled after a foraging visit with probability of 1/2. In the infrequent-refilling treatment, the flowers were also full at the beginning of each observation, but refilling probability was only 1/3. There was no variability in reward among colors in both treatments, except for the seemingly stochastic variability which was generated by the bee's foraging activity. Since all the artificial flowers contained nectar at the beginning of observation, the expected proportion of rewarding flowers diminished gradually during the course of a bee's foraging activity in these treatments. Further details on the flowers and experimental setup are supplied in Keasar et al., 1996.

DATA ANALYSIS

Under our null hypothesis, the complete foraging record of each bee is expected to contain equal proportions of foraging visits to each of the flower colors. This expectation was tested in the following manner: the significance of the deviations of the observed visits distribution from this equal-proportion expectation was tested separately for each bee using a G-test ($df = 2$). Bees were considered to forage nonrandomly with respect to color (i.e., to be *selective*) if the null hypothesis was rejected with $p < 0.05$. The most frequently visited color was determined for each bee. The number of bees with a significant preference for bee-blue, bee-green, and bee-blue-green was then counted. Some bees visited two of the colors to a similar degree, and strongly discriminated against the third color display. When counting the frequencies of preference to the three displays, we considered such bees to contribute half a score to each of their preferred colors.

The magnitude of the deviation from random color choice was quantified by computing, separately for each bee, the equitability index

$$J = \frac{-\sum_{i=1}^3 P_i \ln P_i}{\ln(3)}.$$

The numerator of J is the Shannon–Weaver diversity index, with the P_i 's denoting the proportion of visits to the different colors. The denominator is the maximal possible value of the Shannon–Weaver index in our experiments. The resulting ratio ranges from zero to one, with 0 indicating exclusive visits to one color and 1 indicating equal choice of all color morphs.

RESULTS

COLOR CHOICES IN ENTIRE FORAGING RECORDS

More than 50% of the bees foraged nonrandomly with respect to color (Fig. 3), although flowers of the different color displays were identically rewarding. Bees which preferred the bee-blue flowers were more abundant than bees which preferred bee-blue-green and bee-green in most of the treatments. However, the null hypothesis of random choice of the three colors could not be rejected in any of the treatments. It could also not

be rejected when data from all treatments were pooled ($G = 0.66$, $df = 2$, NS). The frequency of preference for different colors was not associated with the source colony of the bees (G -test for independence, $G = 16.41$, $df = 12$, $0.10 < p < 0.50$). The frequencies of departure from random color choice, and the magnitude of this departure, varied with experimental treatment. They were highest when the different colors were placed in separate clusters, lower when they were placed in adjacent clusters, and lowest when they were randomly intermingled (Fig. 3). Nonrandom color choice was also more frequent and more pronounced when the artificial flowers were always rewarding than when offering rewards according to a probabilistic schedule (Table 2, Fig. 3).

COLOR CHOICES AT THE BEGINNING OF THE FORAGING SESSION

Fifty percent of all the bees with nonrandom color choices made their first foraging visit to a bee-blue flower, 23% to a bee-green flower, and 27% to a bee-blue-green flower (Fig. 4a). These figures refer only to visits which included head insertion into the artificial flowers, since cases of landing without probing were not recorded. The deviation from the 1/3, 1/3, 1/3 distribution which is expected under a first-order null model of

Table 2a

The magnitude of color preferences for the different treatments, as expressed by the equitability index J . For each treatment, the second column presents the mean of the empirical J over all bees in that treatment, and the third column presents the mean of the average simulated J over all bees in that treatment. The fourth column presents the t -value for comparing these means, and the fifth column presents the two-tailed p -value. See Methods for details of computation

Treatment	Empirical J	Average simulated J	t -value	p -value
Separate clusters	0.84	0.93	$t_{19} = -2.18$	0.042
Adjacent clusters	0.93	0.97	$t_{18} = -1.73$	0.101
Intermingled	0.98	0.99	$t_{21} = -2.23$	0.037
Frequent refilling	0.92	0.92	$t_{18} = 0.19$	0.851
Infrequent refilling	0.96	0.95	$t_{20} = 0.69$	0.498

Table 2b

The magnitude of color preferences for the different treatments, as expressed by the proportion of selective bees. For each treatment, the second column presents the empirical proportion of selective bees, and the third column presents the mean of the simulated proportion of selective "bees" over all bees in that treatment. The fourth column presents the t -value for comparing these means, and the fifth column presents the two-tailed p -value. See Methods for details of computation

Treatment	Empirical proportion of selectives	Simulated proportion of selectives	t -value	p -value
Separate clusters	0.75	0.74	$t_{19} = 0.03$	0.976
Adjacent clusters	0.58	0.51	$t_{18} = 0.61$	0.549
Intermingled	0.32	0.10	$t_{21} = 2.28$	0.033
Frequent refilling	0.58	0.71	$t_{18} = -1.24$	0.231
Infrequent refilling	0.57	0.68	$t_{20} = -1.42$	0.171

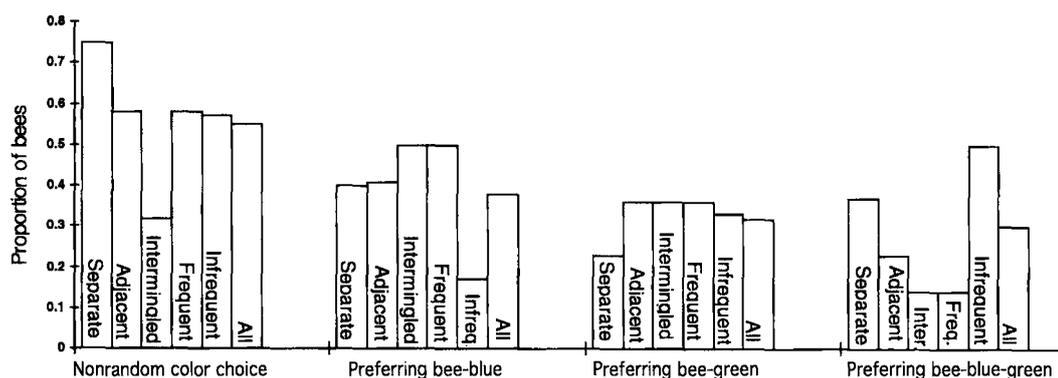


Fig 3. Summary of the frequency of nonrandom color choices in the experimental treatments. Frequency of color preference was calculated by dividing the number of bees with statistically significant nonrandom color choice by the total number of bees in the treatment. The proportions in the three rightmost columns were computed by dividing the number of bees with a particular color preference by the total number of bees which made nonrandom color choices. Flower refilling probabilities were 1 for the separate clusters, adjacent clusters, and intermingled treatments; 1/2 for the frequent-refilling treatment; and 1/3 for the infrequent-refilling treatment. The column "All" shows combined data from all the experimental treatments.

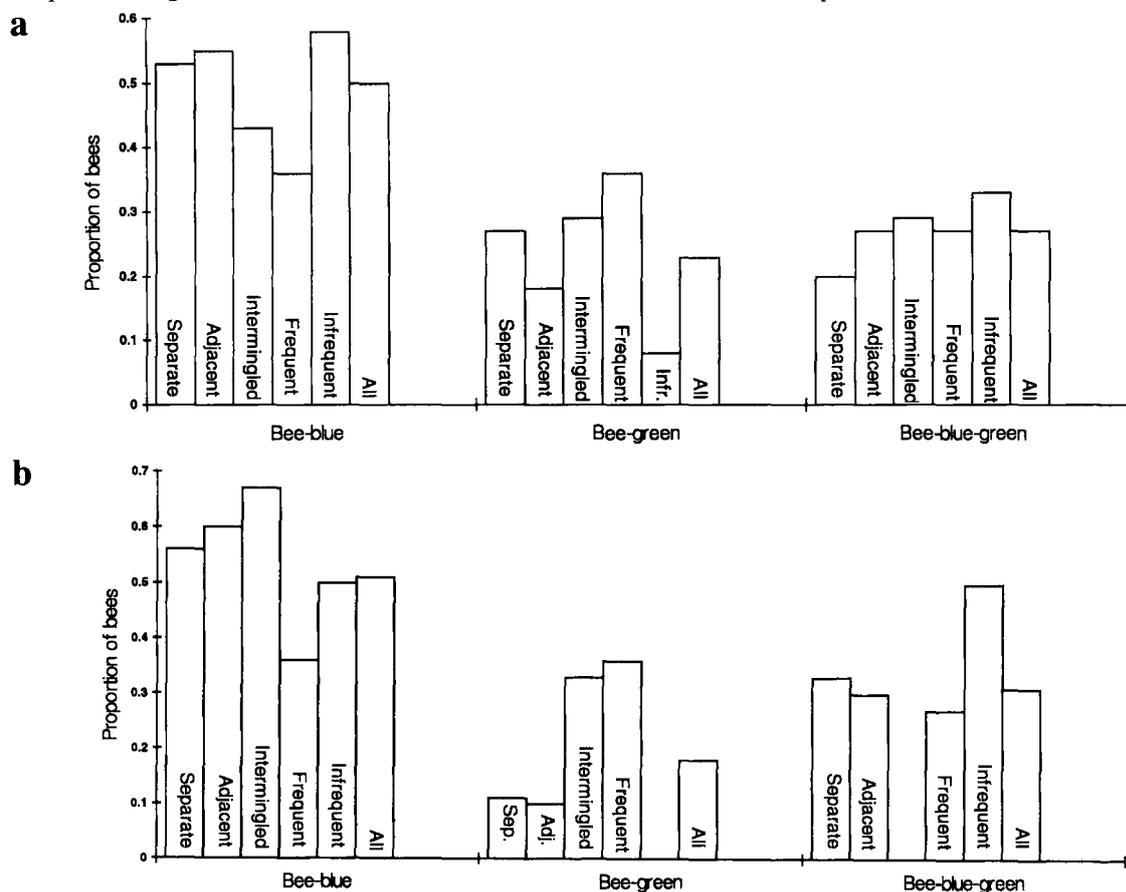


Fig. 4. The frequency of a first visit (a) and three consecutive first visits (b) to a bee-blue, bee-green, or bee-blue-green flower in the different experimental treatments. Only bees which foraged nonrandomly in respect to color were included in the analyses, in order to allow comparison with Table 2. The column "All" shows combined data from all the experimental treatments.

random color choice is statistically significant ($G = 6.74$, $df = 2$, $p < 0.05$). In order to test whether the preference for human-blue persisted beyond the first

visit, we considered separately the cases where all three first visits of a bee were to one color. We counted how many of these bees made their early visits to each of the

colors (Fig. 4b). The distribution of color choices was biased in favor of bee-blue in this analysis as well ($G = 6.66$, $df = 2$, $p < 0.05$).

MODELING THE BEES' COLOR CHOICES

We now looked for a mechanism to explain why the color choices of some bees deviate from the expected 1/3, 1/3, 1/3 distribution. An obvious deviation from random choice by the bees was their tendency to make "runs" of consecutive visits to the same color (Table 3), i.e., to persist on the same color for a period of time during the foraging bout. We suspected that the existence of monocolour runs can account for some of the bees' nonrandom color choices. Therefore we tried a "black box" approach, where we incorporated monocolour runs into a simple simulation model of color choice. Then we compared the predictions of this model with the color choices which were observed in the experiments. In the first step of the simulations, colors were chosen with unequal probabilities: bee-blue was chosen with probability 0.50, bee-green with probability 0.23, and bee-blue-green with probability 0.27. These probabilities are the experimentally-determined frequencies for a first visit to each of the three colors (Fig. 4a). In an additional set of simulations, we gave each of the colors an equal probability to be visited in the first step. This change did not have a noticeable effect on the results of the simulation. Next the simulation was given a "persistency" parameter $0 < a < 1$. A similar persistency parameter is included in a learning model by Roth and Erev (1995). From then on, at each step, a random number between 0 and 1 was generated. If it was larger than a , then the next color was again chosen at random with probabilities 1/3, 1/3, 1/3. Otherwise, the same color that had been chosen in the previous step was chosen again. Thus, the overall probability that the same color will be chosen again is $p = a + \frac{1}{3}(1 - a)$, which will lead to an average run length of $1/(1-p)$. The bees' runs were simulated in this manner as obtained from a geometric distribution, higher values of a

creating longer runs. In other words, to simulate the behavior of a bee with an average run length l ,

$$a = 1 - \frac{3}{2l}.$$

We computed the average run length for each bee, and used this input to generate 1000 simulations of color-choice sequences, each comprised of 150 visits, for that bee. We calculated the equitability index J for each simulation in order to estimate the strength of the deviation from equal choice of the three colors. Thus we obtained 1000 simulated values of J for each bee, and calculated their average (Table 2a). We then tested the hypothesis that the means of the average simulated- J and the empirical value of J (obtained from experimental data) are the same, using a t -test for paired observations (since the average simulated J and the empirical J for each bee are not independent). Likewise, we determined for each simulation whether or not the "simulated bee" was a selective one (according to whether or not the G -test for equal proportions of color choice was rejected at the 0.05 significance level). We thus obtained, for each bee, the proportion of simulations where the "simulated bee" turned out to be selective (Table 2b), and used a t -test for paired observations to test the hypothesis that the means of simulated proportion and the empirical proportion of selective bees are the same.

The results of this analysis indicate that if we take the bees' tendency to perform "runs" into consideration, the empirical data do not deviate from the expected under random choice in most of the cases.

Next we tried to understand the specific color preferences in our experiments; for example, why a particular bee preferred the green flowers while another favored the blue flowers. Differences between bees in the preferred color may result from a random color-choice process, as in our simulation model. But they may also result from differences in the bees' foraging experience. In particular, we considered the possibility of an early learning effect at the beginning of the foraging session. Namely, that an initial, brief exposure to one of the three available colors could lead to a preference for that color from that point on, due to the formation of a learning association between color and reward. Such an association would drive the subsequent foraging choices of the bees.

In order to search for a possible early learning interval in the course of the experiment, we arbitrarily divided the bees' flower visits into initial, middle, and final periods (visits 1–50, 51–100, and 101–150, respectively). We looked at each bee's color choices during different groups of visits in the initial period, and compared them with the color choices in the final period. As a control, we performed the same comparisons on our

Table 3

Mean (\pm SE) number of consecutive visits, "run" length to one color in the different treatments. One bee in the frequent refilling treatment differed markedly from other bees by making 140 consecutive visits to the same color. Mean "run" length for this treatment, with the outlying bee excluded, is given in parentheses

Treatment	Mean "run" length
Separate clusters	9.83 \pm 1.14
Adjacent clusters	3.65 \pm 0.19
Intermingled	1.46 \pm 0.05
Frequent refilling	11.56 \pm 3.62 (8.04 \pm 0.86)
Infrequent refilling	7.22 \pm 0.49

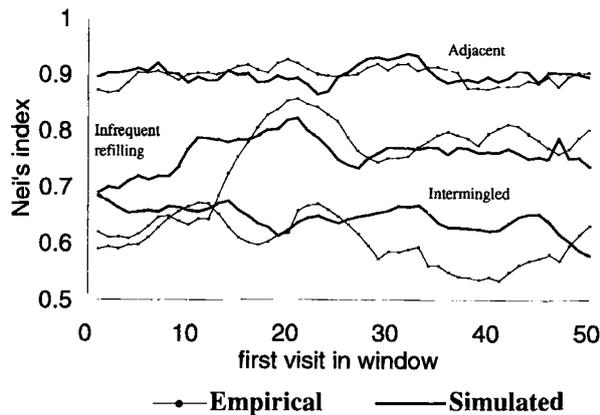


Fig. 5. Nei similarity index between the bees' initial and final color choices for empirical (thick lines) and simulated (thin lines) sequences of color choice. In this example we compared the initial color choices of each bee within a "sliding window" of 11 visits (color choices during visits 1–11, 2–12 ... 50–61) with color choices during its final 50 visits. The uppermost empirical line is the mean Nei index for all of the bees in the adjacent-cluster treatment (mean run length 4.14). The corresponding simulated line is the Nei index for one randomly selected, simulated color choice sequence with the same run length. The same procedure was used for the infrequent-refilling treatment (middle lines) and the intermingled treatment (bottom lines). Nei index values for the separate-cluster and frequent-refilling treatments lie within the range of the plotted data, and are in good agreement with the corresponding simulated values. These are not shown here, for the sake of graphical clarity.

simulated color choice sequences. The resemblance between the bees' color choices at the beginning of the foraging session and those at the end of it was measured using Nei's similarity index (Nei, 1972)

$$I_L = \frac{\sum x_i y_i}{\sqrt{\sum x_i^2 y_i^2}}$$

where x_i and y_i are the proportions of visits to color i during a bee's early flower visits, and its last visits, respectively.

We expected that a critical learning period in the empirical data, if it exists, would be characterized by a higher Nei index than the simulation data. We experimented with different sizes of the early learning period (between 3 and 15 flower visits), and with different starting times of the critical period (between the bees' 1st and 50th visit). The similarity in color choice patterns between the initial period and final period did not differ markedly between empirical data and simulated data in any of our analyses. One such analysis is presented as an example (Fig. 5).

DISCUSSION

The color choices in our experiment varied widely between individual bumblebees. Some bees visited all of the colors with similar frequencies, as expected by our null hypothesis. The majority of the bees, however, foraged nonrandomly with respect to color and showed color preferences. Can the observed color preferences be explained by our alternative hypotheses, i.e., the innate-attraction hypothesis or the searching-efficiency hypothesis?

Choice of bee-blue was significantly more frequent than random during the bees' first three visits. This suggests that the bees did have an initial preference for bee-blue over bee-green and bee-blue-green. This choice pattern is clearly consistent with our innate-attraction hypothesis. Moreover, the preference for blue color is also consistent with previous findings pointing out an innate preference for blue in honeybees (Giurfa et al., 1995), and rapid learning of blue by experienced bees (Menzel, 1967). The possible adaptive value of inborn color attraction has been discussed by Giurfa et al. (1995). However, the preference for blue may also have resulted from a generalization process, in which the bees chose colors according to their perceptual similarity with the pretraining, human-grey feeder (Giurfa, 1991). This latter possibility thus provides another alternative hypothesis which is worth testing in further experiments.

The number of bees which favored bee-blue, bee-green, and bee-blue-green was approximately equal when entire foraging records were considered. This pattern emerged for each experimental treatment separately, and for the pooled data of all treatments. It seems that the bees' initial attraction to blue was modified by their later experience, as may be expected for innate preferences in a pollinator that needs to cope with a changing environment. Such preferences should be weak enough to allow the learning of new information. The color choices of bumblebees in our experimental array were also partially consistent with our second alternative, searching-efficiency hypothesis. This hypothesis predicts that bees will forage persistently in one of the available flower colors, but different bees may prefer different colors, as was indeed observed in our experiments.

The monochlor runs observed can be interpreted as a partially constant foraging behavior, because other flower types are meanwhile ignored by the foraging bees. It has been repeatedly suggested that constancy is an outcome of the limited capability of pollinators to learn more than one floral type at a time (Lewis 1986, 1993; Waser, 1986; Laverty, 1994). However, Menzel

(1969) has demonstrated that bees can efficiently learn several colors trained in a sequence at the feeding site. Another possibility is that provided by Greggers and Menzel (1993) and Chittka et al. (in press) who worked with honeybees and bumblebees, respectively. These authors showed correlations between the probability of flights between different colored feeders (Greggers and Menzel, 1993) or flower species (Chittka et al., in press), and the duration of flight. Both studies showed that within a short time window of the first 3 s of flight time between two successive visits, bees tend to perform more constant flights. If flight time exceeds 4–5 s, they tend to switch. A possible interpretation is that, if a similar feeder appears in the next 3 s after leaving the last one, it will be chosen, and constant behavior will be observed; if such a feeder does not appear in the next 4–5 s after leaving the last one, bees will tend to switch. This makes sense because a forager that spends excessive time in searching for a particular food type that is difficult to find wastes energy and time and becomes less selective. Interestingly, this latter possibility may be directly related to our finding that the spatial distribution of flowers (and thus flight time between them) drastically affects the occurrence of constant or non-constant foraging behavior. We demonstrated that flower clustering and constant reward schedules increased the frequency and magnitude of color-preference formation, while intermingled flowers with a probabilistic feeding schedule promoted a more random color choice. Both of these factors decreased the bees' tendency to switch flower color, and caused them to make longer series of consecutive visits to flowers of the same morph. A similar effect of distance on flower constancy in honeybees is described by Marden and Waddington (1981). Such results can thus be partially interpreted in the frame of Greggers and Menzel's (1993) and Chittka et al.'s (in press) findings.

In an attempt to understand the basis for differences in color preference between bees, we considered the possibility that the bees' first foraging visits to the artificial flowers affected their ultimate color preferences. We failed to find support for this idea in our results since the early color choices of the bees in our experiments were as similar to their final color choices as in the simulated, randomly generated data sets. A possible interpretation for this negative result is that the early learning period that should be considered for analyses is not that occurring at the beginning of the foraging session with the three-color array; rather, important learning may have taken place during pretraining with the human-grey feeder. Although all of the bees were exposed to the same grey feeder, their visits to it were not

monitored, and probably varied in extent and timing among individuals. It is possible that this variation contributed to the variability between bees in color preferences during the color-choice testing. Giurfa et al. (1995) have shown that the amount of experience on achromatic, "neutral" color signals drastically influences the subsequent color choices of honeybees. Thus, observed differences could be due, at least partially, to this factor.

The detailed learning mechanism which determines the bees' choices and run lengths is still unknown, and understanding it is an important challenge (Real, 1991; Menzel et al., 1993). Our attempts to fit some of the published learning algorithms (e.g., Rescorla and Wagner, 1972; Harley, 1981; Greggers and Menzel, 1993; Roth and Erev, 1995) to our experimental data have not been successful so far. Nevertheless, some insight can be gained if the existence of monocolour runs is incorporated into a model of bee decision-making. Our simulations demonstrate that the mere inclusion of monocolour runs into a color-choice model is sufficient to create a certain level of color preference, even if the a priori probabilities for starting a "run" are equal for the three colors. However, the color preference which is predicted by this model is weaker, in some cases, than the preference which was observed experimentally (Table 3). This suggests that the existence of monocolour runs may contribute to the formation of color preferences in additional, indirect ways. Possibly, monocolour runs may facilitate the formation of search images (Shettleworth et al., 1993) or they may consolidate the bees' memory for the last-visited color (Menzel et al., 1993). Thus, although the mechanism which determines run-length still has to be elucidated, monocolour runs may also contribute to the development of *active* color preferences in the bees. The effects of flower clustering and reward predictability on the formation of color preferences are consistent with interpretations which involve search-image and memory formation.

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