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**FLIGHT DURATIONS IN BUMBLEBEES
UNDER MANIPULATION OF FEEDING
CHOICES**

by

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Flight durations in bumblebees under manipulation of feeding choices

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ABSTRACT

Foraging bees spend less time flying between flowers of the same species than between individuals of different species. This time saving has been suggested as a possible advantage of flower-constant foraging. We hypothesized that the time required to switch flower type increases if (a) such switches are infrequent and (b) the bees need to decide whether to switch or not. Bumblebees were taught to forage on artificial feeders that were identical in morphology and reward schedule, but differed in the color of their landing surface. In the first two experiments bees foraged alternatively between two feeders. The landing surface was manipulated to coerce the bees to perform either a color-constant or a color-shift flight movement. In Experiment 1 the landing surfaces were switched every 2-3 visits, while in Experiment 2 they were switched every 6-7 visits. In the third experiment, the bees were required to decide whether to make a color-constant or a color-shift flight.

Inter-visit time was defined as time elapsed between consecutive visits to feeders. When feeder colors were changed frequently (Experiment 1), we detected no difference between color-constant and color-shift inter-visit times. When bees were repeatedly exposed to one color (Experiment 2), color shifts required a significantly longer time. When allowed to choose (Experiment 3), bees performed more color-constant flights than color-shift flights. Inter-visit times were similar for color-constant and color-shift flights in this experiment. Inter-visit times in Experiment 3 were significantly longer than in Experiment 2, and slightly but non-significantly longer than in Experiment 1.

The results suggest that bees indeed save time through flower-constant foraging. Although this time saving is small (~ 1 s / flower visit), and appears only when switches between flower types are infrequent, it may provide a selective advantage to flower-constant foraging.

Keywords: bees; decision making; flight time; flower constancy; handling time; search image

INTRODUCTION

Several species of bees (e.g. Waddington, 1983), butterflies (Lewis, 1989, Goulson et al., 1997) and hoverflies (Goulson & Wright, 1998) forage in a flower-constant manner. That is, they direct most of their foraging visits in a single trip to one flower species, ignoring other rewarding species that they encounter (Waser, 1986). In bees, different individuals within the same species or colony may be constant to different plant species (Heinrich, 1976). Bees show higher constancy to plants that are locally abundant (Chittka et al., 1997, Stout et al, 1998) or that distinctly differ in color from their neighbors (Waser, 1986, Kunin, 1993, Wilson & Stine, 1996, Chittka et al., 1997).

Flower constancy apparently reduces foraging efficiency, since it often causes foragers to forego feeding opportunities, and to travel longer distances to their food sources. It is therefore assumed that flower-constant foraging results from some kind of constraint on the foraging abilities of bees (Chittka et al., 1999). One possible constraint involves the bees' need to learn the morphology and handling technique for each of their forage plants (Lavery, 1994). It has been suggested that bees are limited in their ability to learn the handling of more than one flower type quickly and accurately. In other words, the know-how of handling one flower morphology may interfere with the ability to handle a second one (Darwin, 1876). This "interference hypothesis" is supported by the finding that butterflies (Lewis, 1986) and bumblebees (Lavery, 1994, Chittka et al., 1997) perform more slowly on a learned motor task after being trained on a second, different task. On the other hand, the absolute amount of time lost through this interference in bees is rather small (Woodward & Lavery, 1992, Gegear & Lavery, 1995). Moreover, bees that are trained on two motor tasks in alternation eventually learn to execute both of them efficiently (Dukas 1995, Chittka et al., 1997).

A second possible advantage of flower constancy may arise from perceptual constraints on searching efficiency, i.e. from limitations on the abilities of bees to remember and/or search for more than one flower species at a time. This hypothesis may be considered a variant of the "interference hypothesis", since both ideas stress the bees' limitations in learning and memory as a driving force for flower constancy. The two hypotheses differ in the nature of the putative mental constraint: handling of flowers according to the interference hypothesis, searching for flowers according to the searching efficiency hypothesis. The searching efficiency hypothesis received

circumstantial support in a laboratory study of honeybees feeding on four electronic feeders that provided sucrose solution at varying rates. The feeders, each marked by a different color, were placed at the corners of a 1x1 m square. Honeybees that collected sucrose from a feeder could either return to the same feeder, or fly to a different one, on their next visit. The bees spent less time while returning to a feeder they had just visited than when they flew between two different feeders (Greggers & Menzel, 1993). Similarly, bumblebees foraging in a meadow spent a longer time flying between plants of different species than between plants of the same species. (Chittka et al., 1997). These findings were interpreted to indicate that bees search more efficiently for flowers that are similar to the flower they had just left. This could be because bees can process only one search image in their short-term working memory (Menzel, 1999, Chittka et al., 1999), or because the retrieval of a different search image requires the time-consuming activation of long-term memory (Greggers & Menzel, 1993, Chittka et al., 1999). Bumblebees also fly more slowly when searching for small or cryptic food sources than when searching for large or conspicuous one (Goulson, 2000, Spaethe et al., 2001). These findings also suggest that constraints on searching may affect the time budgets of foraging bees.

A third possible constraint favoring flower constancy in bees is that the morphology of floral pollen may allow efficient packing of monospecific pollen in the bees' corbiculae, while heterospecific pollen may be transported less efficiently (Zahavi et al., 1983). The role of this possible limitation in promoting flower-constant foraging has not yet been sufficiently investigated.

The three possible constraints mentioned above are not mutually exclusive. In the present study we focus on one of them - the searching efficiency hypothesis - as a possible selective factor favoring flower constancy. We investigated the time costs of information processing for foraging bees. First, we hypothesized that frequent switching between floral displays would be time consuming for bees. Although bees learn to associate visual and chemical cues with food rewards within 1-3 trials (Menzel, 1982), they may require several consecutive encounters with a floral display to search for it efficiently. We therefore expected that flight durations would be shorter when bees encounter the same display several times in succession than when the display type is switched frequently.

Secondly, we hypothesized that the need to choose what floral display to visit next would be time consuming for bees. Dietary specialization is associated with faster

foraging in aphids, presumably because simpler decision-making is involved (Bernays & Funk, 1999). The reduced cost of decision-making was suggested as a general advantage of dietary specialization in animals, including flower constant foraging by insects (Bernays, 1999). Following this reasoning, we expected that flight durations of bees would be longer if they are required to choose between two food sources, as compared with a situation where only one food source is available at a time.

METHODS

General

The experimental system and laboratory are described in detail in Keasar (2000). Experiments were carried out in a 3×4 m flight room. Temperatures ranged from 26-30° C, and relative humidity was 40-70%. The room was illuminated during 06:30-18:30 by 6 pairs of D-65 fluorescent lights. Experiments were conducted during April-September 1998, March-June 1999 and November-December 1999. Colonies of naïve *Bombus terrestris* (L.) were obtained from Kibbutz Yad Mordechai, Israel. The queens of the colonies were treated by the suppliers to forego hibernation. Pollen was supplied *ad lib.*, directly to the colony. The bees were allowed to fly freely around the room between experiments. During the experiments, only one bee, marked by a number tag, was allowed to forage at a time. Computer-controlled artificial feeders were used for the experiments. All feeders had a removable colored plastic landing surface that could be replaced during the experiment. A 30% sucrose solution was used in the feeders as nectar substitute, and the feeders dispensed ca. 1 microliter per visit. Once a bee left a feeder, it was automatically refilled. Landing surfaces were wiped with a clean paper towel after each visit, while the bee was at another feeder. This was done to remove any possible scent marks that could affect the bee's future foraging behavior (Giurfa & Nunez, 1992; Giurfa, 1993; Gilbert al., in press). When a switch of landing surface was needed (see experimental design below), it was also performed when the bee was away from the feeder. Thus, wiping and switching of landing surfaces did not interfere with the bees' activity. The computer recorded the time whenever a bee inserted its proboscis into a feeder. Bees from five colonies were used, and each bee participated in one experiment only. Each bee was pre-trained, and then allowed to conduct 200 visits to the artificial feeders. The experiments were performed by two observers.

Pre-training

Identical pre-training was performed before every experiment. Two morphologically identical artificial feeders were set on a green table in the laboratory flight room, 30 cm apart. Green landing surfaces (maximum reflectance at 520 nm) were placed on the feeders. The bees were trained to fly back and forth, foraging first on one feeder and then on the other, for 30 visits. The goals of the pre-training were (1) to expose the bees to the feeders so that they could learn how to manipulate them quickly and effectively (Laverty, 1994a, Gegear & Laverty, 1995); (2) to allow the bees to learn the locations of the feeders; (3) to train the bees to forage alternatively between the two feeders.

Experiment 1 (12 bees)

The same two morphologically identical artificial feeders used in the pre-training were used in the experiment. The removable plastic landing surfaces used in the experiment were blue (maximum reflectance at 460 nm) and yellow (maximum reflectance at 600 nm). The color surfaces were changed in a pattern that caused the bee to make either a color-constant flight or a color-shift flight (Fig. 1). The pattern of color switches was shift-constant- constant -shift- constant -shift-shift etc, i.e. B-Y-Y-Y-B-B-Y-B-B-B-Y-Y-B-Y-Y-Y-B-B-Y-B-B-B-Y-Y (B denotes blue, Y denotes yellow). 50% of the flights were color-constant, while the remaining 50% involved color-shifts. Similarly, the feeder color choices (blue and yellow) were equally divided.

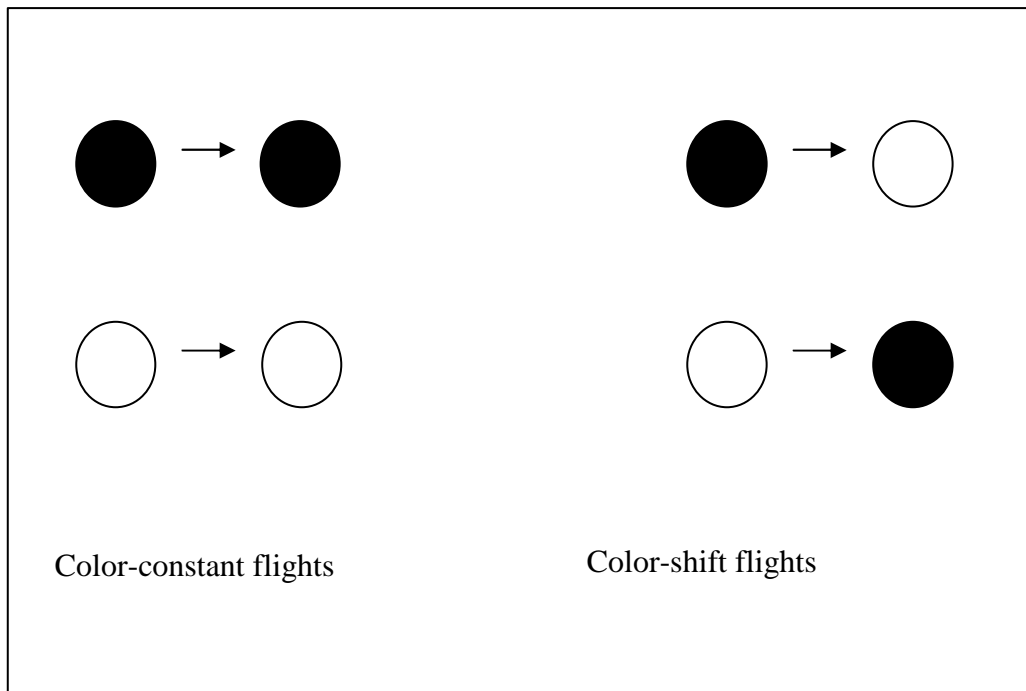


Fig. 1: A schematic description of color-constant and color-shift flights in the experiments. Color-constant flights were between artificial feeders with landing surfaces of the same color, whereas color-shift flights were between feeders that differed in the color of their landing surface.

Experiment 2 (13 bees)

Methods for feeder set-up, flight-time recordings and training period were identical to those in Experiment 1. Experiment 2 differed in the pattern of color switching, which was 6 constant – 1 shift - 7 constant – 1 shift – 7 constant – 1 shift - 6 constant – 1 shift etc, i.e. B-B-B-B-B-B-B-Y-Y-Y-Y-Y-Y-Y-Y-B-B-B-B-B-B-B-B-B-Y-Y-Y-Y-Y-Y-Y etc. Since the bee was consistently exposed to six or seven color-constant flights before shifting color, the ratio between color-constant and color-shift flights was not equal, and was approximately six to one. However, feeder color choices remained equally divided with 50% of the visits to blue feeders, and 50% to yellow feeders.

Experiment 3 (12 bees)

This experiment used four morphologically identical feeders, set up in pairs of two. Each pair consisted of one blue and one yellow feeder. The colors were switched every 6-8 visits in order to change the position of the colors (Fig. 2). The bees were trained as in the previous two experiments. After the pre-training and before the beginning of the experiment, two additional morphologically identical artificial

feeders were placed on the table, next to the existing feeders. This created a situation where the bee, when flying from one feeder, across the table to the other side, is faced with two options (binary choice). While the bee was imbibing on one side of the table, the adjacent feeder was covered, preventing the bee from visiting it.

We assumed that the difference in the distance between the feeder directly opposite (30 cm) and the feeder adjacent to it (30.15 cm) is negligible and would not affect flight time. Experiment 3 differed from the previous experiments in that it involved decision-making, i.e. the bee had to decide whether to make a color-constant or a color-shift flight following each visit.

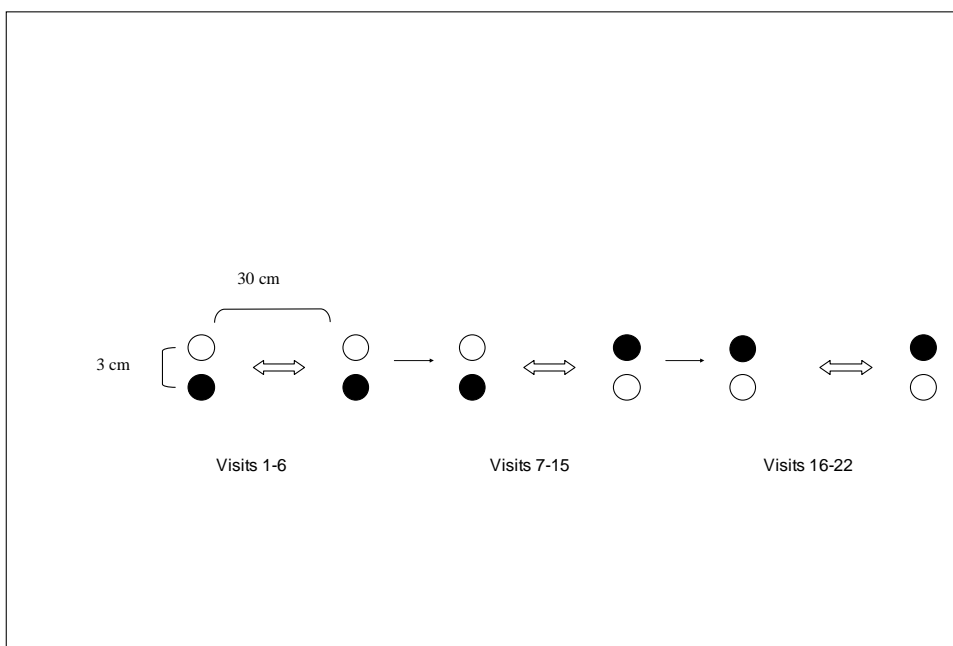


Fig 2: Design of Experiment 3 (example). The bees chose between two feeders, marked blue (filled circles) and yellow (open circles), 3 cm apart, on each foraging visit. Once a bee landed at a feeder, its neighbor was covered until the next foraging choice was made. The thick arrows describe the bees' back and forth movement between pairs of feeders. The locations of the blue and yellow feeders were changed every 6-7 visits, as indicated by the thin arrows.

Data analysis

Inter-visit durations, defined as the time elapsed between proboscis insertion into two consecutive feeders, were calculated for all bees. These durations included the time required to handle a feeder, imbibe its nectar, and fly to the next feeder.

During the course of the experiments we improved our data recording system. These improvements allowed us to record handling durations separately from flight durations for nine of the bees. This detailed recording allowed us to test, by fitting a least-square trend line for each bee, whether handling durations remained constant

throughout the experiment. We also tested whether handling durations differed between color-constant and color-shift flights. We discarded inter-visit durations that were longer than 20 s from the data set. This allowed us to eliminate flights that involved a return to the colony, and exploratory flights around the room. The mean number of inter-visit durations that were shorter than 20 s was 121.88 ± 16.47 (SE) for Experiment 1, 146.08 ± 6.23 for Experiment 2, and 139.25 ± 6.44 for Experiment 3. We tested whether the color (blue or yellow) or location (right or left) of the feeders towards which the bees flew affected inter-visit durations. We tested these hypotheses for each bee separately, using t-tests for experiments 1 and 2, and one-way ANOVAs for Experiment 3. We also tested for effects of the bees' source colony and the identity of the observer on inter-visit durations.

Successive inter-visit durations by the same bee cannot be considered independent data points, since the duration of a bee's early flights may affect the length of her later flights. We therefore conservatively considered the mean duration of color-constant and color-shift flights for each bee as one pair of data points. This yielded 12, 13 and 12 pairs of data points for experiments 1, 2 and 3, respectively. We used paired t-tests to compare the mean duration of color-constant and color-shift inter-visit times within each experiment. Handling durations preceding color-constant and color-shift flights were compared in the same manner for the nine bees with detailed records. We used a similar procedure to test whether bees prefer color-constant to color-shift flights when given a choice: we calculated the proportion of color constant flights for each bee in Experiment 3, and then tested whether the mean proportion differed from 0.5. Thus, each bee contributed a single data point to the test. This procedure eliminates possible effects of dependence between measurements for each individual.

RESULTS

Handling durations

Handling durations were measured separately from flight durations for nine bees (5 in Experiment 2, 4 in Experiment 3). Handling time was not expected to differ between experiments, since all feeders had identical morphology and mechanics. Our results verify this expectation. In addition, no bee showed a significant decrease in handling duration over time during the course of the experiment. Handling times were typically 3-5 s. This result suggests that handling durations over the course of the experiments can be regarded as constant. Handling durations that preceded color-

constant and color-shift flights did not differ significantly ($t=0.652$, $df=8$, $p=0.53$). Thus, differences between color-constant and color-shift inter-visit durations can be attributed to differences in flight times.

Effects of feeder location, color, source colony and observer

In order to test for effects of location, differences in functioning of individual feeders or effects of the lab setup on the bees, we compared inter-visit durations before visiting right and left feeders. In Experiment 1 we found significant differences in time taken to approach right and left feeders in 4 out of the 12 bees. In Experiment 2 we found such differences in 1 out of 13 bees. In Experiment 3, no significant effect of feeder location was found for any of the bees. In experiments 1 and 2, the shorter inter-visit times were sometimes associated with the right feeder, and sometimes with the left feeder. These differences can be ascribed to several reasons. A reasonable possibility is a technical problem with one of the artificial feeders. For example, if the sugar solution in one feeder happened to be shallower or deeper than in its counterpart (and was therefore either harder or easier to reach), handling time would be affected. Another possibility is that something in the setup of the lab, such as the position of the observer (unpublished data) or the locations of landmarks (Chittka et al, 1995), caused the bees to fly faster in one direction than in the other. This explanation seems less plausible, however, as there was no consistently preferred direction. As a precaution, we excluded the data from the five problematic bees from further analysis.

One of the bees that exhibited location bias also exhibited color bias, and spent a significantly shorter time before visiting blue feeders than before visiting yellow feeders. All other 36 bees exhibited no difference in inter-visit time connected to the color of the feeder. Inter-visit times were not affected by the foraging bees' source colony (ANOVA, $n_1=13$, $n_2=7$, $n_3=5$, $n_4=3$, $n_5=9$, $F=1.48$, $P=0.18$), or by the identity of the observer ($n_1=17$, $n_2=20$, $t=0.64$, $P=0.26$ for color-constant flights, $n_1=17$, $n_2=20$, $t=1.63$, $P=0.06$ for color-shift flights).

Color-constant vs. color-shift flight durations

We found no difference between color-constant and color-shift movements in Experiment 1, neither in individual bees nor when they were grouped together (Fig.3),

paired t-test, $t=1.447$, $P=0.088$). In Experiment 2, we found that three out of the 12 bees spent significantly less time during color-constant flights than during color-shift flights. Seven other bees showed a similar trend that was not statistically significant, and the two remaining bees had non-significantly longer inter-visit times during color-constant flights than during color-shift flights (Fig. 4). Color-constant and color-shift flight durations were averaged for each bee and compared. This comparison confirmed that, on the whole, color-constant flights were shorter than color-shift flights in this experiment (paired t-test, $n=12$, $t=2.87$, $P=0.007$). In Experiment 3 there was no significant difference between color-constant and color-shift flight durations in any of the bees, nor when they were grouped together (Fig. 5), paired t-test, $t= -0.504$, $P=0.312$).

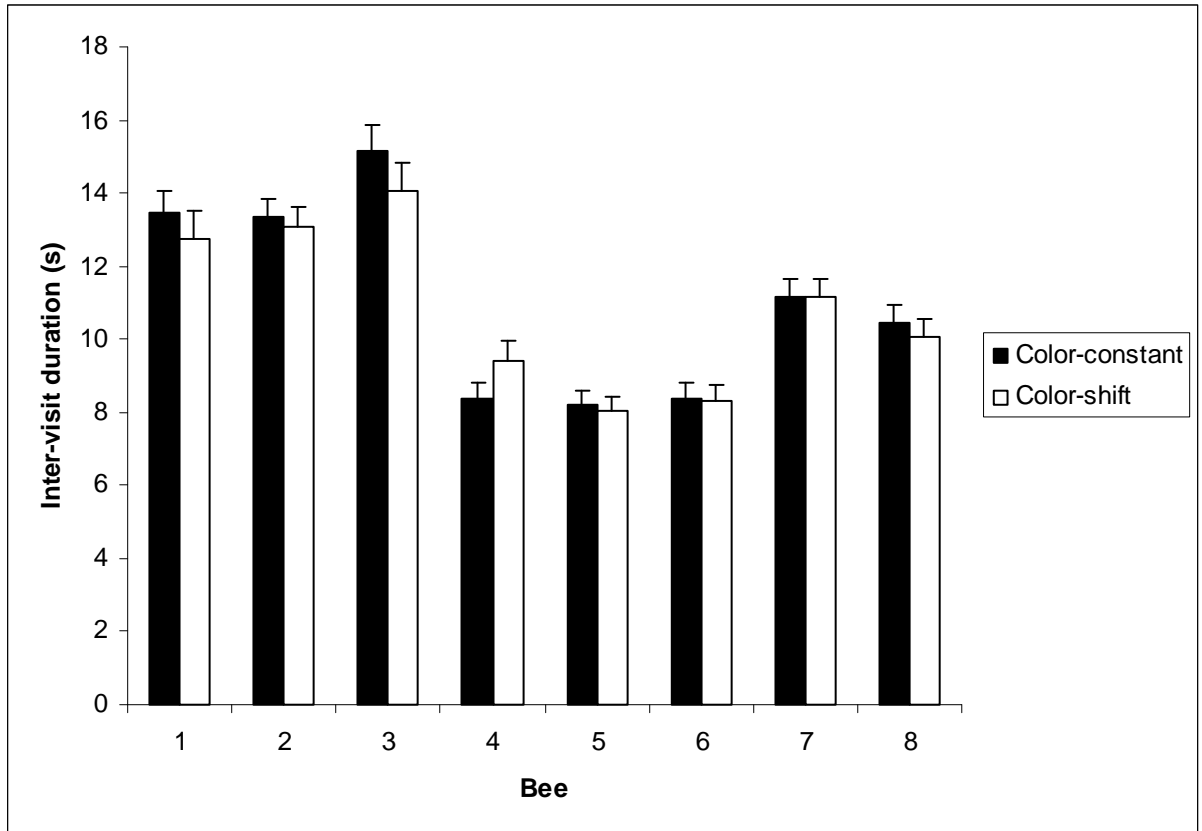


Fig. 3: Mean durations of color-constant (black bars) and color-shift (white bars) inter-visit intervals for individual bees in Experiment 1. Error bars are 1 SE.

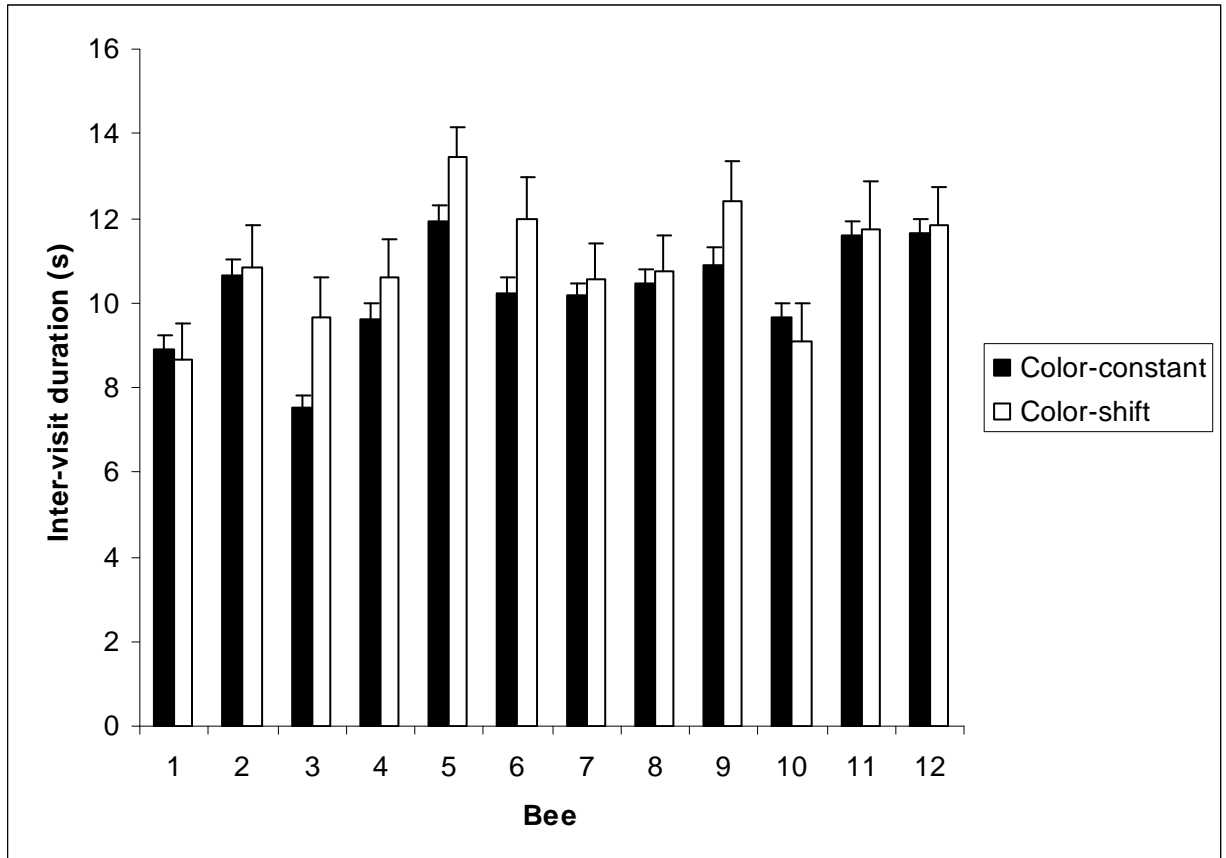


Fig. 4: Mean durations of color-constant (black bars) and color-shift (white bars) inter-visit intervals for individual bees in Experiment 2. Asterisks denote bees with statistically significant differences ($P < 0.05$) between color-constant and color-shift flight durations. Error bars are 1 SE.

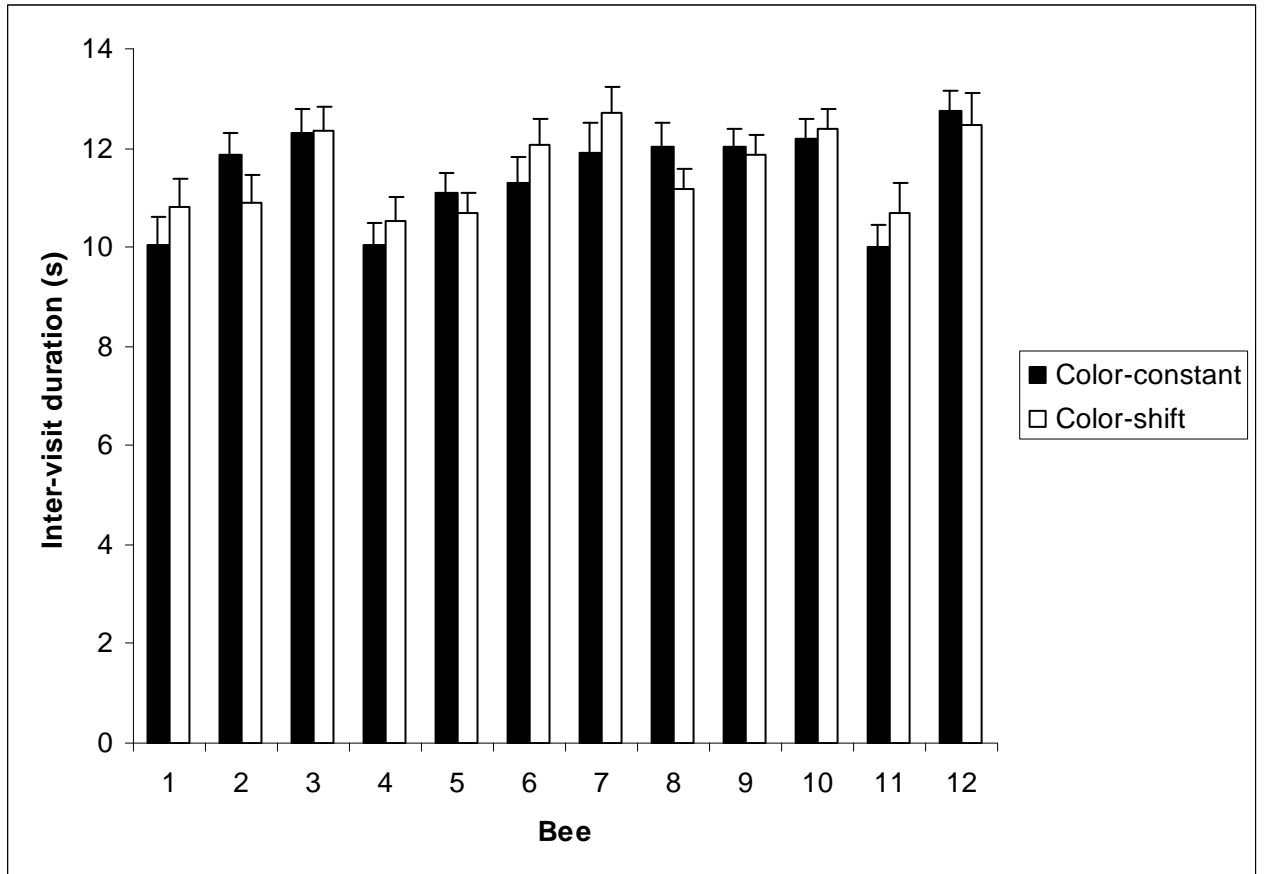


Fig. 5: Mean durations of color-constant (black bars) and color-shift (white bars) inter-visit intervals for individual bees in Experiment 3. Error bars are 1 SE.

Experiment 3: Choice to stay or to shift

When allowed to choose to make either a color-constant or a color shift flight, the bees slightly but significantly preferred color-constant flights to color-shift flights (0.558 ± 0.021 (SE) of all flights, $n=927$ for color-constant flights, $n=735$ for color-shift flights, $t=2.784$, $P=0.009$).

Differences between experiments

We plotted the mean durations for color-constant and color-shift flights for the three experiments in ascending order (Fig. 6). Bees that were required to make choices (Experiment 3) had longer inter-visit intervals than bees that did not make choices. We calculated an standardized inter-visit duration for each bee by averaging between its mean durations of color-constant and color-shift flights. This eliminated the effects of differences in the relative frequencies of color-constant vs. color-shift flights between experiments, since both types of flights were given equal weight. The

standardized inter-visit durations were significantly longer in Experiment 3 than in Experiment 2 ($t=2.035$, $df=22$, $P=0.027$). The differences between Experiment 3 and Experiment 1 were not statistically significant ($t=0.599$, $df=8$, $P=0.283$).

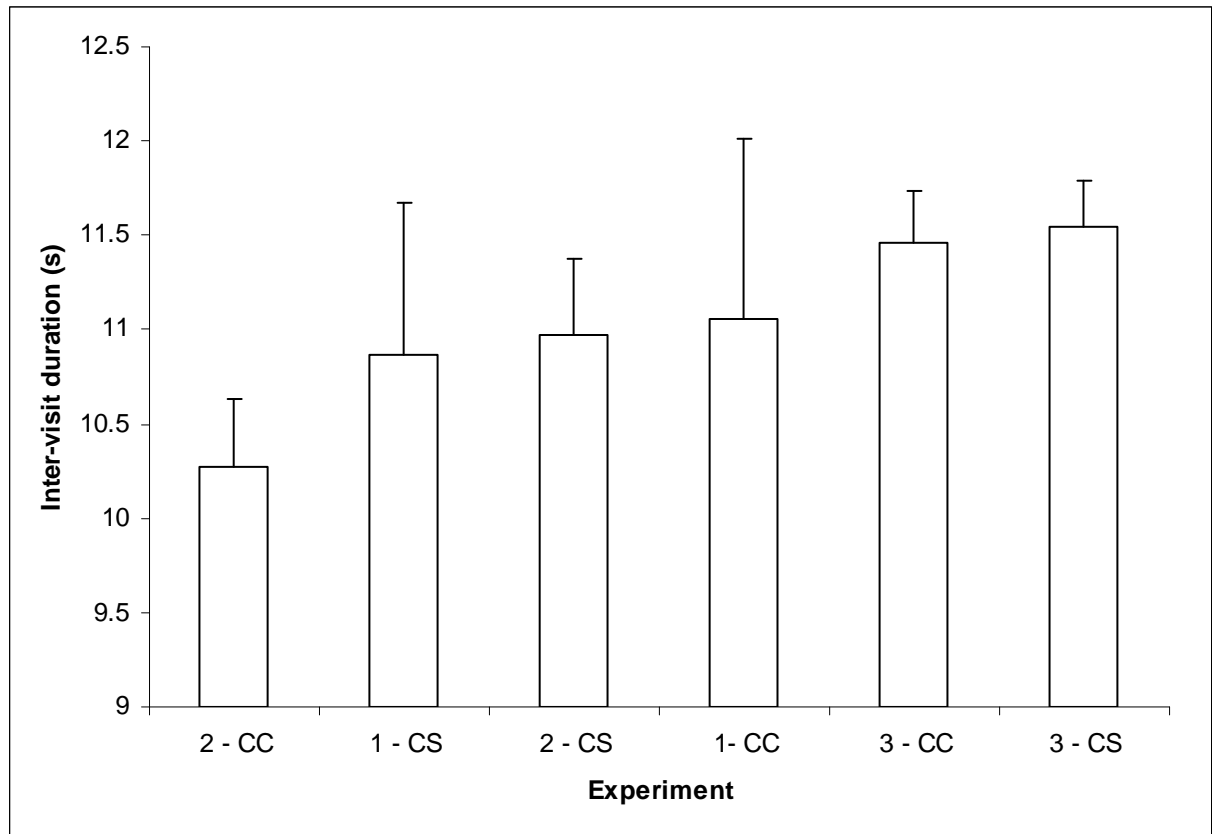


Fig. 6: Mean durations of color-constant (CC) and color-shift (CS) inter-visit intervals in experiments 1-3, averaged over all bees in each experiment. Error bars are 1 SE.

DISCUSSION

Our experiments provide an analysis of flight-time dynamics in foraging bees under more controlled conditions than in previous work. Previous studies measured flight durations of bees that were allowed to make their own foraging choices (Greggers & Menzel, 1993, Chittka et al, 1997). In our experiments 1 and 2, we eliminated possible effects of decision-making on flight durations by either coercing the bees to shift color or to remain color-constant on each visit. Moreover, our experiments controlled for the effects of flight distances and food rewards by keeping them constant.

Handling durations

Previous laboratory (Keasar et al, 1996) and field (Lavery, 1994a, Gegear & Lavery, 1995) studies indicate that bees require 30-100 flower visits (depending on floral complexity) to learn to handle their food sources accurately and quickly. Typically during this learning period, handling time decreases gradually and eventually stabilizes. A similar trend was observed in our experiments. The stable handling durations measured in the present study suggest that the bees learned to handle our simple artificial feeders efficiently during the 30 visits of the pre-training phase.

Color-constant vs. color-shift flight durations

Color-constant flights were significantly shorter than color-shift flights in Experiment 2, but not in experiments 1 and 3. Experiment 2 also differed from experiments 1 and 3 in having a lower frequency of color-shift flights (15% in Experiment 2, 50% and 44% in experiments 1 and 3, respectively). This result is compatible with Chittka et al's (1997) finding that flights between plants of different species are more time-consuming than flights between plants of the same species. Though not explicitly reported, it is likely that the bees in the study of Chittka et al (1997) made several visits to feeders within the same plant before switching to another one. Thus, their data probably relate to cases where switches between species were fairly infrequent, as in our Experiment 2.

There are several possible cognitive explanations for the decrease in flight durations in the color-constant flights of Experiment 2. One possibility is that the bees formed a search image (Tinbergen, 1960) i.e. a mental representation of the artificial feeder that rewarded them during their color-constant flights. This search image may have remained as long as they were presented with the same feeder type, and may have expedited their foraging. The frequent color switches in experiments 1 & 3 possibly interfered with the formation of search images. The use of search images has been described in the foraging behavior of many avians, including blackbirds (Lawrence, 1985), quail (Gendron, 1986), pigeons (Blough, 1989, Reid & Shettleworth, 1992) and blue jays (Dukas & Kamil, 2001). In concordance with our findings, searching for prey in quail was most effective after several successive exposures to the search image (Gendron, 1986). Search images are usually thought to be a mechanism for locating cryptic prey. Rewarding flowers can be cryptic to bees, if they are viewed against a background that contains many other flowers of similar

color (Goulson, 2000). The feeders in our experiment were not cryptic. Nevertheless, successive encounters with the same feeder type allowed the bees to make faster color-constant flights than color-shift flights. This suggests that the mechanism that enabled the bees to forage faster is not limited to the detection of cryptic items.

Alternatively, information processing may be slowed down whenever bees need to pay attention to more than one object at a time, such as when flying from one feeder to a feeder of the other color. This happened much more frequently in experiments 1 & 3 than in Experiment 2, and may have obscured differences between color-constant and color-shift flight durations. The implications of the need to allocate attention to predator avoidance (and to other tasks) during foraging are discussed by Dukas & Ellner (1993) and Dukas & Kamil (2001).

An additional level of interpretation deals with differences in the memory retrieval and data processing tasks between the experiments. In experiments 1 and 3, the bees may have learned to switch regularly between both feeder types, and to keep the properties of both types in their working memory. In experiment 2, color-shifts were infrequent, possibly causing the bees to retain only the image of the currently visited feeder in their short-term working memory. The image of the other feeder may have been stored in a different, more long-term, memory (Menzel, 1999). According to this interpretation, during color-shift flights in experiment 2 the bees were presented with a feeder that did match the image stored in their short-term working memory. This mismatch, and the need to retrieve the feeder image from a more long-term memory, may have caused the observed increase in flight durations (R Menzel, pers. comm.).

According to all three interpretations, the additional time required for color-shift flights is expected to depend on the length and regularity of color-constant sequences encountered by the bee. This prediction can be tested in additional experiments.

Bees that forage on a single flower type may handle the flowers more quickly and accurately than after a period of exposure to a different flower type (Lavery, 1994b). On the other hand, bumblebees that are trained on two motor tasks (e.g. two flower morphologies) in alternation can switch between the tasks without incurring a cost in handling time (Chittka & Thomson, 1997). Our results suggest that a similar mechanism is involved in the determination of flight durations: bees that regularly switch between feeder types (treatments 1&3) learned to do so with no time costs.

The bees in both Experiment 1 and 2 made half of their visits to blue feeders, and half of them to yellow feeders. This design allows to rule out the possibility that a large number of exposures to one of the floral displays *per se* caused the shorter flight durations in Experiment 2. Rather, it must be concluded that the effect is due to the larger number of color-constant flights in Experiment 2.

Choice to stay or to shift

When allowed binary choices, the bees showed a weak but highly significant preference for color-constant choices. Similarly, other studies show that bees make more color-constant flights than expected by random choice when presented with equally rewarding feeders of different colors (Marden & Waddington, 1981, Hills et al., 1997, Keasar et al., 1997). A similar choice pattern appears in pigeons that forage on two types of cryptic prey. Birds that encounter items of one type in a run, and are then allowed to choose between both types, prefer the food type they had just fed on (Reid & Shettleworth, 1992).

Effects of decision-making

Flight durations in Experiment 3 were significantly longer than in Experiment 2, but not significantly longer than in Experiment 1. Thus, our hypothesis that the need to make decisions would carry flight-time costs was only partially supported. Our data analysis gave equal weight to the color-constant and color-shift flights performed by each bee, eliminating possible effects of different frequencies of color shifting between experiments. Therefore, the lower frequency of color-shift flights in Experiment 2 as compared to Experiments 1 & 3 cannot explain the between-experiment differences in flight durations. Decision-making is impaired under time pressure in humans (Svenson & Maule, 1993), and may account for the reduced speed and accuracy of foraging in generalist vs. specialist insect herbivores (Bernays, 1999). In the present experiment, however, decision-making was not always associated with a time cost. Possibly, the decisions required in experiment 3 (always between two equally rewarding feeders at the same locations) were simple enough that they required no extra time of the bees.

Implications for flower-constant foraging

Our results suggest that bees can indeed spend less time in flight, and thereby forage more efficiently, if they remain constant to one flower color. Real flowers differ also in other display traits, such as morphology and odor. These differences may enhance the time saved by remaining faithful to a single flower type. Such time saving should be expected only when switching between flower types is not very frequent, as in our Experiment 2. Thus, only bees that have already made some flower-constant flights would save time by remaining flower-constant. As bees usually visit several flowers on the same plant before leaving for another one, infrequent switching may well be a realistic scenario. The time saving associated with flower-constant foraging was fairly small in our experiment, in the order of 1 second per flower visit. The reduction in flower handling time during flower-constant foraging is of a similar magnitude (Lavery, 1994b). Lavery (1994b) and Chittka et al (1999) suggested that this time saving alone does not suffice to explain the selective advantage of flower constancy. However, our results suggest an additional time saving in flight durations. Taking into account that a bee makes thousands of flower visits daily, the combined savings in handling and flight may accumulate to a significant time period. Bees often spend much more time getting to their preferred food source, bypassing other rewarding source on the way. The advantage conferred by feeder constancy must be large enough to overcome this time and energy cost. The time saving associated with flight and handling durations probably plays a considerable role in this advantage.

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