

Flight Durations in Bumblebees Under Manipulation of Feeding Choices

Noam Bar-Shai,¹ Rana Samuels,¹ Tamar Keasar,^{2,5} Uzi Motro,^{1,3,4} and Avi Shmida^{1,3}

Accepted October 29, 2001; revised October 29, 2003

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. In Experiment 1 the colors of the landing surfaces were switched every two or three visits, while in Experiment 2 they were switched every six or seven visits. In the third experiment, the bees were required to decide whether to make a color-constant or a color-shift flight. Intervisit 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 intervisit 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. Intervisit times were similar for color-constant and color-shift flights in this experiment. Intervisit times in Experiment 3 were significantly longer than in

¹Department of Evolution, Systematics and Ecology, Hebrew University, Jerusalem 91904, Israel.

²Department of Life Sciences, Achva College, Mobile Post Shikmim 79800, Israel.

³Center for Rationality and Interactive Decisions, Hebrew University, Jerusalem 91904, Israel.

⁴Department of Statistics, Hebrew University, Jerusalem 91904, Israel.

⁵To whom correspondence should be addressed. Fax: 972-8-992-6581. e-mail: tkeasar@bgumail.bgu.ac.il.

Experiment 2 and slightly but nonsignificantly longer than in Experiment 1. The results suggest that bees indeed save time though flower-constant foraging but that this time savings is a small (~ 1 s/flower visit) under laboratory conditions, and appears only when switches between flower types are infrequent. The time saved may be more significant over long foraging trips, and when morphological differences between flower species are large, as often happens under natural conditions, providing a selective advantage to flower-constant foraging.

KEY WORDS: 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 and 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 and 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 (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 and Lavery, 1992; Gegeer and 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 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 bees spent less time while returning to a feeder they had just visited than when they flew between two different feeders (Greggers and 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 just left. Bumblebees also fly more slowly when searching for small or cryptic food sources than when searching for large or conspicuous ones (Spaethe *et al.*, 2001). These findings also suggest that constraints on information retrieval (Chittka *et al.*, 1999) 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 one to three 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.

Second, 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 and 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, 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 by Keasar (2000). Experiments were carried out in a 3 × 4-m flight room. Temperatures ranged from 26 to 30°C, and relative humidity was 40–70%. The room was illuminated during 0630–1830 by six 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 μ l per visit. Once a bee left a feeder, it was automatically refilled. Landing surfaces were wiped with a clean paper towel, moistened with water, 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 (Stout and Goulson, 2001, 2002). 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 pretrained, then allowed to conduct 200 visits to the artificial feeders. The experiments were performed by two observers.

Pretraining

Identical pretraining 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. During this pretraining session, after the bee left one of the feeders it was immediately covered, so that only the other feeder was accessible for foraging. The

goals of the pretraining were (1) to expose the bees to the feeders so that they could learn how to manipulate them quickly and effectively (Laverty, 1994a; Gegebar and Laverty, 1995), (2) to allow the bees to learn the locations of the feeders, and (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 pretraining 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. 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). Fifty percent of the flights were color-constant, while the remaining 50% involved color shifts. Similarly, the feeder color choices (blue and yellow) were equally divided.

Experiment 2 (13 Bees)

Methods for feeder setup, flight-time recordings, and training period were identical to those in Experiment 1. Experiment 2 differed in the pattern of color switching, which was six constant–one shift–seven constant–one shift–seven constant–one shift–six constant–one shift, etc., i.e., B–B–B–B–B–B–Y–Y–Y–Y–Y–Y–Y–Y–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. The color-switching schedule forced each bee to make both color-constant and color-shift flights, which allowed comparison between the two types of flight within the same individual.

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 six to eight visits in order to change the position of the colors (Fig. 1). The bees were trained as in the previous two experiments.

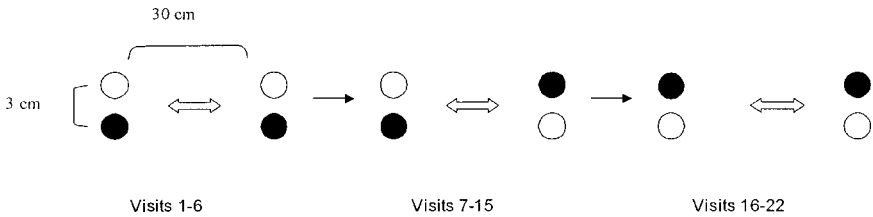


Fig. 1. Design of Experiment 3 (example). The bees chose between two feeders, marked blue (filled circles) and yellow (open circles), 3 cm apart, on each foraging visit. Once a bee landed at a feeder, its neighbor was covered until the next foraging choice was made. The thick arrows describe the bees' back-and-forth movement between pairs of feeders. The locations of the blue and yellow feeders were changed every six or seven visits, as indicated by the thin arrows.

After the pretraining 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.

Data Analysis

Intervisit 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 (five in Experiment 2, four in Experiment 3). This detailed recording allowed us to test, by fitting a least-squares 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-shifts flights. We discarded intervisit 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 intervisit 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.

Successive intervisit 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 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 intervisit 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 of the proportions differed from 0.5. We used cluster sampling methods (Steel and Torrie, 1981) to calculate the mean proportion, since the values in each data series (color-constant and color-shift flights for each bee) are not independent variables. 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. Mean handling times were 5.58 ± 0.44 (SE) s. 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. The slopes of the individual best-fit lines that describe the change in handling durations with experience ranged from -0.018 to 0.006 , and none of them differed significantly from zero. This finding 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 ($t_8 = 0.652$, $P = 0.53$). Thus, differences between color-constant and color-shift intervisit durations can probably be attributed to differences in flight times.

Color-Constant vs. Color-Shift Flight Durations

We found no difference between color-constant and color-shift movements in Experiment 1 (paired *t*-test, $t_{11} = 1.447$, $P = 0.088$). In

Experiment 2, color-constant flights were shorter than color-shift flights ($t_{12} = 2.87$, $P = 0.007$). In Experiment 3 there was no significant difference between color-constant and color-shift flight durations ($t_{11} = -0.504$, $P = 0.312$).

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 (mean proportion of color-constant flights, 0.558 ± 0.021 [SE]; $t_{11} = 2.784$, $P = 0.009$).

Differences Between Experiments

We plotted the mean durations for color-constant and color-shift flights for the three experiments in ascending order (Fig. 2). Bees that were required to make choices (Experiment 3) had longer intervisit intervals than bees that did not make choices. We calculated a standardized intervisit 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 intervisit durations were significantly longer in Experiment 3 than in Experiment 2

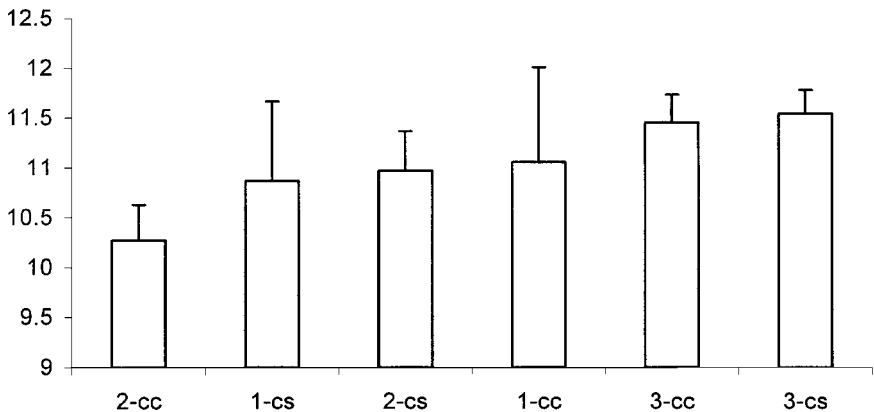


Fig. 2. Mean durations of color-constant (CC) and color-shift (CS) intervisit intervals in Experiments 1–3, averaged over all bees in each experiment. Error bars are 1 SE.

($t_{22} = 2.035$, $P = 0.027$). The differences between Experiment 3 and Experiment 1 were not statistically significant ($t_{18} = 0.710$, $P = 0.243$).

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 and Menzel, 1993; Chittka *et al.*, 1997). In our Experiments 1 and 2, we eliminated possible effects of decision-making on flight durations by coercing the bees either 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 (Laverty, 1994a; Gegear and Laverty, 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. 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 pretraining 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 by Chittka *et al.* (1997) made several visits to flowers 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 and 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 and Shettleworth, 1992), and blue jays (Dukas and 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 and 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 and Ellner (1993) and Dukas and 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 not 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, personal communication).

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 and 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 and 3) learned to do so with no time costs.

The bees in both Experiment 1 and Experiment 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 and 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 just fed on (Reid and Shettleworth, 1992).

Effects of Decision-Making on Flight Durations

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 compared to Experiments 1 and 3 cannot explain the between-experiment differences in flight durations. Decision-making is impaired under time pressure in humans

(Svenson and 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, of the order of 1 s per flower visit. The reduction in flower handling time during flower-constant foraging is of a similar magnitude (Laverty, 1994b). Laverty (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 time getting to their preferred food source, bypassing other rewarding source on the way. As bumblebees have been shown to fly at 5–7 m/s, they can cover much ground in a short time (Osborne *et al.*, 1999). Therefore, the small time-saving of being flower-constant may be equivalent to hundreds of meters in transit time, which suggests an additional advantage to flower constancy. The advantages conferred by flower constancy must be large enough to overcome its time and energy cost. The time savings associated with flight and handling durations probably plays a considerable role in these advantages.

ACKNOWLEDGMENTS

This study was supported by the Israeli Science Foundation and by the Center for Rationality and Interactive Decisions at the Hebrew University.

Sharon Shafir participated in the planning of the experiments. We are grateful to R. Menzel for helpful comments on the manuscript.

REFERENCES

- Bernays, E. A. (1999). Plasticity and the problem of choice in food selection. *Ann. Entomol. Soc. Am.* **92**: 944–951.
- Bernays, E. A., and Funk, D. J. (1999). Specialists make faster decisions than generalists: Experiments with aphids. *Proc. Roy. Soc. Lond. Ser. B* **266**: 151–156.
- Blough, P. M. (1989). Attentional priming and visual search in pigeons. *J. Exp. Psychol. Anim. Behav. Proc.* **15**: 358–365.
- Chittka, L., Geiger, K., and Kunze, J. (1995). The influences of landmarks on distance estimation of honeybees. *Anim. Behav.* **50**: 23–31.
- Chittka, L., Gumbert, A., and Kunze, J. (1997). Foraging dynamics of bumblebees: correlates of movements within and between plant species. *Behav. Ecol.* **8**: 239–249.
- Chittka, L., Thomson, J. D., and Waser, N. M. (1999). Flower constancy, insect psychology and plant evolution. *Naturwissenschaften* **86**: 361–377.
- Darwin, C. (1876). *Cross and Self-Fertilization in the Vegetable Kingdom*, Murray, London.
- Dukas, R. (1995). Transfer and interference in bumblebee learning. *Anim. Behav.* **49**: 1481–1490.
- Dukas, R., and Ellner, S. (1993). Information processing and prey detection. *Ecology* **74**: 1337–1346.
- Dukas, R., and Kamil, A. C. (2001). Limited attention: the constraint underlying search image. *Behav. Ecol.* **12**: 192–199.
- Gegeer, R. J., and Laverty, T. M. (1995). Effect of flower complexity on relearning flower-handling skills in bumblebees. *Can. J. Zool.* **73**: 2052–2058.
- Gendron, R. P. (1986). Searching for cryptic prey: Evidence for optimal search rates and the formation of search images in quail. *Anim. Behav.* **34**: 898–912.
- Giurfa, M. (1993). The repellent scent-mark of the honeybee *Apis mellifera ligustica* and its role as communications cue during foraging. *Insectes. Soc.* **40**: 59–67.
- Goulson, D. (2000). Are insects flower constant because they use search images to find flowers? *Oikos* **88**: 547–552.
- Goulson, D., Ollerton, J., and Sluman, C. (1997). Foraging strategies in the small skipper butterfly, *Thymelicus flavus*: When to switch? *Anim. Behav.* **53**: 1009–1016.
- Greggers, U., and Menzel, R. (1993). Memory dynamics and foraging strategies of honeybees. *Behav. Ecol. Sociobiol.* **32**: 17–29.
- Heinrich, B. (1976). The foraging specializations of individual bumblebees. *Ecol. Monogr.* **46**: 105–128.
- Hills, P. S. M., Wells, P. H., and Wells, H. (1997). Spontaneous flower constancy and learning in honey bees as a function of colour. *Anim. Behav.* **54**: 615–627.
- Keasar, T. (2000). The spatial distribution of non-rewarding artificial flowers affects pollinator attraction. *Anim. Behav.* **60**: 639–646.
- Keasar, T., Motro, U., Shur, Y., and Shmida, A. (1996). Overnight memory retention of foraging bumblebees in imperfect. *Anim. Behav.* **52**: 95–104.
- Keasar, T., Bilu, Y., Motro, U., and Shmida, A. (1997). Foraging choices of bumblebees on equally-rewarding artificial flowers of different colors. *Israel J. Plant Sci.* **45**: 219–229.
- Kunin, W. E. (1993). Sex and the single mustard—Population density and pollinator behavior effects on seed set. *Ecology* **74**: 2145–2160.
- Laverty, T. M. (1994a). Bumblebee learning and flower morphology. *Anim. Behav.* **47**: 531–545.
- Laverty, T. M. (1994b). Costs to foraging bumblebees of switching plant species. *Can. J. Zool.* **72**: 43–47.
- Lawrence, E. S. (1985). Evidence for search image in blackbirds (*Turdus merula* L): Short-term learning. *Anim. Behav.* **33**: 929–937.
- Lewis, A. C. (1986). Memory constraints and flower choice in *Pieris rapae*. *Science* **232**: 863–865.

- Lewis, A. C. (1989). Flower visit constancy in *Pieris rapae*, the cabbage butterfly. *J. Anim. Ecol.* **58**: 1–13.
- Marden, J. H., and Waddington, K. D. (1981). Floral choices by honeybees in relation to the relative distances to flowers. *Physiol. Entomol.* **6**: 431–435.
- Menzel, R. (1982). Short-term memory in the honey bee. In *The Biology of Social Insects*, Westview Press, Boulder, pp. 356–359.
- Osborne, J. L., Clark, S. J., Morris, R. J., Williams, I. H., Riley, J. R., Smith, A. D., Reynolds, D. R., and Edwards, A. S. (1999). A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *J. Appl. Ecol.* **36**: 519–533.
- Reid, P. J., and Shettleworth, S. J. (1992). Detection of cryptic prey: Search image or search rate? *J. Exp. Psychol. Anim. Behav. Proc.* **18**: 273–286.
- Spaethe, J., Tautz, J., and Chittka, L. (2001). Visual constraints in foraging bumblebees: Flower size and color affect search time and flight behavior. *Proc. Natl. Acad. Sci. USA* **98**: 3888–3903.
- Steel, R. G. D., and Torrie, J. H. (1981). *Principles and Procedures of Statistics, a Biometrical Approach*, McGraw–Hill, New York.
- Stout, J. C., and Goulson, D. (2001). The use of conspecific and interspecific scent marks by foraging bumblebees and honeybees. *Anim. Behav.* **62**: 183–189.
- Stout, J. C., and Goulson, D. (2002). The influence of nectar secretion rates on the responses of bumblebees (*Bombus* spp.) to previously visited flowers. *Behav. Ecol. Sociobiol.* **52**: 239–246.
- Stout, J. C., Allen, J. A., and Goulson, D. (1998). The influence of relative plant density and floral morphological complexity on the behaviour of bumblebees. *Oecologia* **117**: 543–550.
- Svenson, O., and Maule, A. (1993). *Time Pressure and Stress in Human Judgment and Decision Making*, Plenum Press, New York.
- Tinbergen, L. (1960). The natural control of insects in pinewoods. *Arch. Neerland. Zool.* **13**: 259–379.
- Waddington, K. D. (1983). Floral-visitation-sequences by bees: Models and experiments. In Jones, C. E., and Little, R. J. (eds.), *Handbook of Experimental Pollination Biology*, Van Nostrand Reinhold, New York, pp. 461–473.
- Waser, N. M. (1986). Flower constancy: definition, cause and measurement. *Am. Nat.* **127**: 593–603.
- White, D., Cribb, B. W., and Heard, T. A. (2001). Flower constancy of the stingless bee *Trigona carbonaria* Smith (Hymenoptera: Apidae: Meliponini). *Austr. J. Entomol.* **40**: 61–64.
- Wilson, P., and Stine, M. (1996). Floral constancy in bumble bees: Handling efficiency or perceptual conditioning? *Oecologia* **106**: 493–499.
- Woodward, G., and Laverty, T. M. (1992). Recall of flower handling skills by bumble bees: A test of Darwin's interference hypothesis. *Anim. Behav.* **44**: 1045–1051.
- Zahavi, A., Eisikowitch, D., Kadman Zahavi, A., and Cohen, A. (1983). A new approach to flower constancy in honey bees. In *Veme Symposium International sur la Pollinisation*, Versailles, INRA, pp. 89–95.