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Measurement of Nest Cavity Volume by the Honey Bee (*Apis mellifera*)*

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Summary. 1. Honey bee swarms exercise considerable care when selecting a nest site. One nest site variable evaluated by bees is cavity volume.

2. The volume distribution of natural nests (Fig. 1) has a wide range (12 to 443 l observed), but most nest volumes are clustered in the 20- to 100-l subrange. The modal volume is approximately 35 l. This distribution reflects a process of volume selection among potential nest cavities when a swarm chooses its nest site. For example, swarms prefer 40-l to 10 and 100-l nest cavities. In nature, the volume-selection process operates primarily by rejecting undersized cavities, but also by rejecting oversized cavities.

3. The observed limit in resolution power of volume perception was discrimination between cubes differing by 15 l.

4. A swarm's preference in nest cavity volume is independent of swarm size.

5. A scout bee's inspection of a nest site spans approximately 40 min. During this time a scout spends most of her time at the nest site, engaged in numerous brief inspections inside and outside the nest cavity. When inside a cavity, a scout's principal behavior is rapid walking about the cavity's inner surfaces. The pattern of walking movements over successive interior inspections shows (1) a general progression from walking mostly near the entrance to walking deeper inside the cavity, and (2) a tendency to traverse different regions of the cavity's interior surface on different inspections.

6. Honey bees can measure cavity volume if at least one of two conditions is fulfilled: (1) the cavity interior is well illuminated, or (2) the cavity's inner surfaces can be completely traversed by walking. The natural conditions for volume perception are probably low (<0.5 lux) cavity illumination, but traversable inner surfaces. The importance of walking to volume perception was demonstrated by manipulating scout bees' perceptions of a cavity's volume by varying the amount of walking required to move between points inside the cavity. The hypothesis is presented that scouts measure the volumes of dimly illuminated cavities by integrating information on the distances and directions of walking movements made inside the cavity.

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* Dedicated to Professor Karl von Frisch on the occasion of his 90th birthday

Introduction

A honey bee colony reproduces by casting forth a swarm – the old queen plus several thousand workers – and rearing a new queen for the parent colony. The swarm leaves the parent colony in a mad whirl but quickly forms a quiet cluster on a tree branch. Scout bees then fly from this cluster in search of a suitable cavity in which to build new combs and set up housekeeping. Because the scouts first locate many possible nest sites before choosing the best one for their new home, the selection of the future nest site frequently continues for several days.

Lindauer (1955, 1961) identified several criteria by which bees evaluate potential dwelling places: protection from wind and sun, dryness, freedom from ants, sturdiness, and distance from the parent colony. Lindauer also reported that scout bees would inspect but reject very small and very large cavities, such as a mouse hole and a large storage box, and he conducted a simple experiment in which a small swarm rejected his nestboxes until he halved the volume of one, whereupon the swarm promptly inhabited the reduced nestbox. These observations suggest that honey bees also measure cavity volume when evaluating potential nest sites. Furthermore, Seeley and Morse (1976) found that the cavity volumes of natural honey bee nests exhibit a clustered distribution.

These suggestive studies prompted the two principal questions addressed in this paper: (1) do honey bees exercise a preference in nest cavity volume? and if so, (2) how do honey bees measure cavity volume?

Materials and Methods

The honey bee swarms used in this study were either wild swarms from unidentified feral colonies around Ithaca, New York, or artificial swarms prepared from colonies of Dyce Laboratory, Cornell University, Ithaca, New York. All honey bees in the Ithaca area are hybrids of the many honey bee races imported for American apiculture. These include primarily *Apis mellifera ligustica* Spinola, *A. m. caucasica* Gorbatschew, *A. m. carnica* Pollmann and *A. m. mellifera* L. Each year many honey bee queens are introduced from the southern and western U.S. into the Ithaca area by the approximately 100 hobby and three commercial beekeepers of this region. Therefore the bees used in these experiments may represent a cross-section of North American honey bees.

Additional methodological details will be provided with the descriptions of individual experiments.

Results

1. Volume Distribution of Natural Nests

Before experiments could be designed to analyze the volume perception process, the volume distribution of natural nests had to be determined. The methods and results of volume measurements on nests in trees were reported by Seeley and Morse (1976). To these data I now add the results of volume measurements

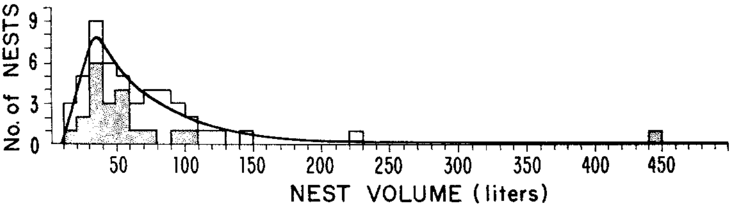

Fig. 1. Volume distribution of natural nests. *Shaded portion* denotes nests in trees; *clear portion* represents nests in man-made structures. $N=49$

of natural nests in man-made structures (walls of buildings, birdhouses and discarded wooden boxes). Determining the volumes of these invariably right-angled and planar-sided nests simply involved exposing each nest and measuring the inner dimensions of its nest cavity.

The results are shown in Figure 1. The curve in this figure is a least-squares fit to points centered in the top of each histogram bar. This distribution of nest volumes shows that the modal volume is 30 to 40 l, that few nests (6%) are smaller than 20 l, that most nests (80%) fall in the 20- to 100-l range, and that nests can be quite large (maximum observed: 443 l) but that such large nests are relatively rare.

2. *Test of Volume Selection*

The earlier evidence for nest volume selection by honey bees is inconclusive. Lindauer's (1955, 1961) observations of scouts inspecting but rejecting very small or very large cavities and Seeley and Morse's (1976) description of the clustered distribution of natural nest volumes provide only suggestive evidence. Even Lindauer's experiment in which a small swarm first rejected a full-sized nestbox but later accepted a half-sized one lacks sufficient controls, such as for cavity shape and interior temperature. The following experiments provide a more rigorous test of volume selection.

The test has two stages. First, swarms are offered a choice between cubical nestboxes of various volumes and their preference is recorded. The second stage then tests whether or not true volume selection produced the apparent volume preference observed in the first stage.

a) Materials and Methods

Nestboxes were constructed of 1.5-cm-thick plywood and were painted dark green on the outside. Each nestbox had a 3-cm diameter entrance hole positioned midway across the front side, 8 cm up from the base. A nail driven horizontally across the entrance prevented occupation by birds. Each nestbox floor was removable to permit interior inspections. In final preparation of the nestboxes, a 4 × 4 cm piece of old honey comb was placed inside each nestbox and the seam between the removable floor and the rest of the nestbox was sealed with opaque photographic tape.

Nestboxes were set out in groups along hedgerows. I refer to a set of nestboxes located together along a hedgerow as a "nestbox station". Each nestbox station had one nestbox of each volume required for a particular experiment. Considerable care was exercised in establishing the nestbox stations. First, four or two sites (the number depending on the experiment) were selected which I judged were approximately equivalent in visibility, exposure, height (at least 3 m off-ground) and separation (at least 25 m). Then using a random number system, I assigned a nestbox to each site. Finally the nestboxes were hoisted into position and nailed securely in place with special attention paid to the alignment of entrance directions and the equalization of entrance heights. Thus nestbox stations were established in which the nestboxes were approximately matched in location and exposure, and in which the different-volumed nestboxes were randomly ordered in linear arrays.

The nestbox stations were established in the vicinity of Ithaca, New York. I monitored the stations by weekly inspections throughout the summer swarming season (May 15 to July 15) and by two inspections during the fall swarming season (August 15 to September 15; Burgett and Morse, 1974). Whenever a nestbox was occupied, the interiors of the other nestboxes in the same nestbox station were inspected. Inhabitants in any of the other nestboxes would have modified the swarm's choice among nestboxes.

The swarms which occupied the nestboxes were all wild swarms of unknown origin. Most swarms probably came from feral colonies which flourish in the woods about Ithaca (Seeley, unpubl. data).

b) Control Experiments

Measuring the honey bee's preference in nest cavity volume by offering swarms arrays of various volumed nestboxes required two preliminary tests of the experimental design.

Temperature Tests on Nestbox Interiors. Temperature differences inside nestboxes of different volumes could influence the choice among nestboxes. To test for such differences the interior temperatures of three pairs of 10- and 100-l nestboxes were monitored after they were positioned in their nestbox stations. A Tel-Tru model GT-100 thermometer was mounted through one side of each nestbox. The average temperature difference between the 10-l and 100-l nestboxes, measured hourly throughout one day, was 0.4° C (SD 0.3°). It seems highly unlikely that such a small difference between the interior temperatures of different-sized nestboxes would bias the nestbox choice.

Test of Simultaneous Nestbox Inspections. A nestbox station consisted of a linear array of different volume nestboxes spaced at least 25 m apart. In designing this experimental layout it was assumed that scouts would inspect all the nestboxes of a station before choosing one of them. To test this assumption two stations with 10-, 40-, 70- and 100-l nestboxes were established 1100 m apart. A natural swarm was collected and placed on a wooden cross (150 cm high with a cross member 50 cm long) between the two stations, 250 m from one and 1000 m from the other. Then I lightly spray-painted the dorsal surfaces of the bees bright orange while they were in their swarm cluster. Thus I could recognize scouts from this swarm wherever I might encounter them.

Within 24 h of setting out the swarm I observed scouts from the swarm at all the nestboxes of both nestbox stations, thereby demonstrating the simultaneous inspection of all the nestboxes in a nestbox station.

c) Volume Preference among Cubical Nestboxes

10-, 40-, 70-, 100-Liter Choice. In the first phase of measuring the volume preference with cubical nestboxes, I provided a choice among 10-, 40-, 70- and 100-l nestboxes. These volumes represent points on the volume distribution for natural nests which are below modal, modal, and above modal (two values), respectively. Fourteen nestbox stations were established and 12 swarms moved into nestboxes of 11 different stations. No other organisms occupied nestboxes of the stations which received honey bee swarms[1]. Therefore 11 swarms experienced a complete choice among 10-, 40-, 70- and 100-l nestboxes. Their occupation distribution was as follows (nestbox volume – number of occupations): 10-0, 40-4, 70-3, 100-4. This demonstates an avoidance of the 10-l nestbox ($P<0.05$, binominal probability), but fails to show any significant preference among the 40-, 70- and 100-l nestboxes. The twelfth swarm inhabited a 70-l nestbox following an earlier swarm's occupation of the 40-l nestbox in the same nestbox station.

40-, 100-Liter Cloice. In this experiment ten stations, each with a 40- and a 100-l nestbox, were established. Because each station used only two nestboxes, in this experiment I was able to equalize more precisely the exposures of the nest sites in a nestbox station, than in the last experiment where each station included four nest sites. Seven swarms occupied nestboxes of seven different stations. Only 40-l nestboxes were occupied, thereby demonstrating a preference of the 40-l over the 100-l nestboxes ($P<0.008$, binomial probability).

In summary, if given a choice among cubical nestboxes 10, 40 and 100 l in volume, with all other factors equal, swarms will prefer the 40-l nestbox. Also, the preference of the 40 over the 10 appears considerably stronger than the preference of the 40 over the 100. These results could be predicted from the volume distribution of natural nests assuming this distribution reflects a preference in nest cavity volume.

d) Test of Volume Selection

The preference tests of the preceding section do not by themselves demonstrate volume selection because the cubical nestboxes, while differing in volume, also differed in lower order properties such as height (first-order) and horizontal cross-section area (second-order).

To distinguish whether volume selection or selection based on some lower-order property had been operating, I again conducted choice experiments using 40-l and 100-l nestboxes, but this time with nestboxes shaped like right parallelepipeds. Figure 2 systematically compares the dimensional properties of the nestboxes involved in these experiments. The logic of the test for volume selection runs as follows. If the previously demonstrated preference of a 40-l cube over 10- and 100-l cubes reflects a preference in some first- or second-order property

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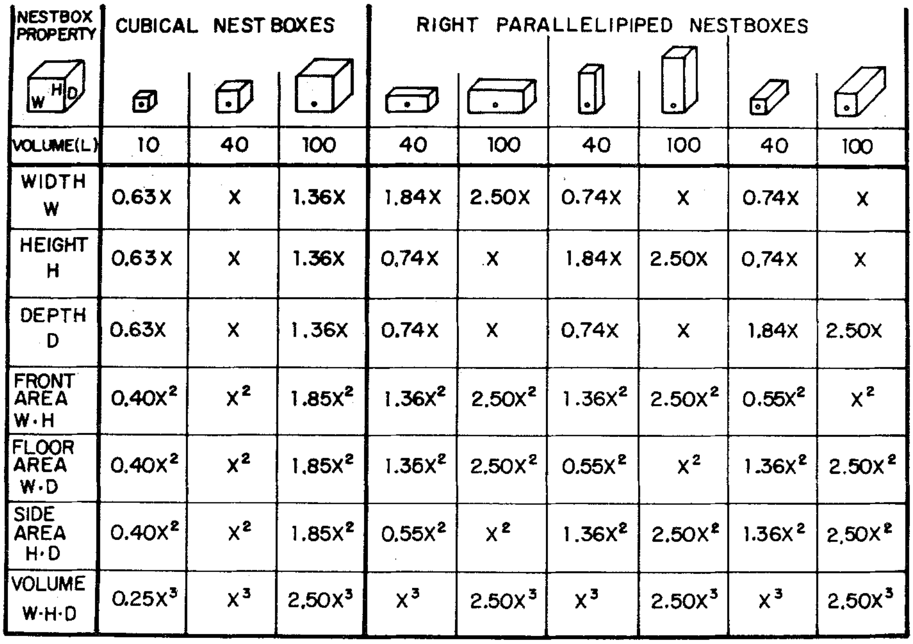
[1] The 40-l nestbox in one station which received no swarms was inhabited by a colony of *Crematogaster lineolata* ants



NESTBOX PROPERTY	CUBICAL NESTBOXES			RIGHT PARALLELEPIPED NESTBOXES					
W H D									
VOLUME(L)	10	40	100	40	100	40	100	40	100
WIDTH W	0.63X	X	1.36X	1.84X	2.50X	0.74X	X	0.74X	X
HEIGHT H	0.63X	X	1.36X	0.74X	X	1.84X	2.50X	0.74X	X
DEPTH D	0.63X	X	1.36X	0.74X	X	0.74X	X	1.84X	2.50X
FRONT AREA W·H	$0.40X^2$	X^2	$1.85X^2$	$1.36X^2$	$2.50X^2$	$1.36X^2$	$2.50X^2$	$0.55X^2$	X^2
FLOOR AREA W·D	$0.40X^2$	X^2	$1.85X^2$	$1.36X^2$	$2.50X^2$	$0.55X^2$	X^2	$1.36X^2$	$2.50X^2$
SIDE AREA H·D	$0.40X^2$	X^2	$1.85X^2$	$0.55X^2$	X^2	$1.36X^2$	$2.50X^2$	$1.36X^2$	$2.50X^2$
VOLUME W·H·D	$0.25X^3$	X^3	$2.50X^3$	X^3	$2.50X^3$	X^3	$2.50X^3$	X^3	$2.50X^3$

Fig. 2. Comparison of the dimensional properties of the cubical and right parallelepiped nestboxes used in the tests of volume selection. All properties are expressed in terms of X, the side length of the 40-l cube-shaped nestbox

of the 40-l cube, then when given a choice between 40- and 100-l parallelepipeds the bees should select the 100-l parallelepipeds, for only these share values with 40-l cubes in any first- or second-order properties. Alternatively, if the preference among cubical nestboxes reflects a preference for the third-order property (volume) of the 40-l cube, then in the choice between 40- and 100-l parallelepipeds, only the 40-l parallelepipeds should be chosen for only these nestboxes share the value of the third-order property (volume) with the 40-l cubes.

The choice tests using 40- and 100-l parallelepiped nestboxes were conducted on Appledore Island, Maine. The experimental layout on the island and the procedures for preparing the artificial swarms used on the island are described in Section 5.a. Six trials were performed. Each trial used a new 1-kg swarm and a new pair of nestboxes. The nestboxes were constructed as described in Section 2.a. Two trials were made for each of the three orientations (see Fig. 2) of the nestboxes. To control for positional bias, the positions of the 40- and 100-l nestboxes were reversed between sites B and D (see Fig. 3) between trials. A swarm's preference between the two nestboxes was indicated in two ways: (1) by the heavy buildup in scouts at one site, and (2) ultimately by the swarm's flight *en masse* toward one of the nestboxes.

In all six trials the swarms chose the 40-l nestbox. By the reasoning delineated above, this preference for the 40-l right parallelepipeds ($P < 0.02$, binomial probability) demonstrates that the preference for 40-l cubes over 10- and 100-l cubes reflects a volume preference, and not a preference in some lower-order property.

3. Resolution Power of Volume Perception

Two measurements of the honey bee's resolution power in volume perception were made while testing for volume selection. In preferring 40- to 100-l nestboxes ($P<0.008$, binomial probability) and in preferring 40- to 10-l nestboxes ($P<0.07$, binomial probability), the bees resolved 60-l and 30-l differences, respectively. To further test the resolution power, I offered swarms choices between 25-l and 10-l nestboxes, and between 25-l and 17.5-l nestboxes. These volumes were used because the volume distribution of natural nests (Fig. 1) suggests there is a sharp boundary between unacceptable and acceptable nest volumes at the lower end of the distribution. If so, then this is where honey bees must resolve volume differences most finely. The materials and methods for these experiments are described in Section 2.a. Ten nestbox stations were used in each of the two resolution tests. All nestboxes were cubical.

Four swarms moved into four stations of the 10–25 test. All four swarms inhabited 25-l nestboxes, thereby demonstrating the bee's ability to resolve this 15-l difference ($P<0.07$, binomial probability). Four swarms occupied nestboxes of three stations in the 17.5–25 test. At all three stations the 25-l nestbox was inhabited, but at one of these stations the 17.5-l nestbox was also occupied. I do not know, for the doubly occupied station, which nestbox was first inhabited. Thus I do not know whether the 25- or the 17.5-l nestbox was actually chosen by a swarm. Of course, only the first swarm to move in would have had a choice between the two nestboxes. Therefore, with only two known selections of the 25-over the 17.5-l nestbox, the bee's ability to resolve a 7.5-l difference is neither disproven nor significantly ($P=0.25$, bionmial probability) substantiated.

4. Volume Preference and Swarm Size

Wild swarms of honey bees vary widely in size, from several hundred to several tens of thousands of individuals (Burgett and Morse, 1974). To see if a swarm's preference in cavity volume is a function of swarm size, I compared swarm size and nestbox volume for swarms which occupied nestboxes of a range of volumes. This data was generated in the volume preference (Section 2.c.) and volume resolution (Section 3) experiments. Swarm populations were measured to the nearest thousand by killing the swarm in the nestbox at night with cyanide, collecting the nestbox and then, in the laboratory, weighing the dead bees shaken from the nestbox. Mitchell's (1970) figure of 7700 bees/kg was used to convert weighings to population values. Population estimations were performed within one week of each swarm's occupation of its nestbox. Therefore a swarm's population would have changed very little between the times of nestbox selection and population measurement.

The data for seven swarms are shown in Table 1. The regression coefficient of swarm population (in thousands) on nestbox volume (in l) is -0.0043 ± 0.0010 (95% confidence intervals). Thus for the swarms observed, the volume of the nestbox inhabitated was essentially independent of swarm size. However, this

Table 1. Comparison of nestbox volume and swarm population

Nestbox Volume (l)	Swarm Population
25	16,000
25	9000
40	7000
40	12,000
70	28,000
70	15,000
100	5000

independence may not hold for very small swarms. Lindauer (1955, 1961) reported that dwarf swarms with populations of probably less than 1000 bees rejected nestboxes which larger swarms had previously accepted, but one dwarf swarm accepted a nestbox after he had halved its volume.

5. *Mechanism of Volume Perception*

The preceding experiments treated the process of volume perception like a "black box". They examined the products of its operation without studying its mechanisms of operation. Through the following experiments I analyzed one feature of the mechanisms of volume perception: the sensory mode(s).

a) Materials and Methods

Location. In order to identify the sensory mode(s) of volume perception, I needed to test the bee's behavior with a diverse array of experimental nestboxes. These nestboxes were far less attractive as home sites than natural nest sites. Therefore, for these experiments I needed a location as devoid as possible of natural nest sites, for only under conditions of little competition would my second-class, experimental nestboxes receive serious attention from scout bees.

This basic requirement in the experimental design was fulfilled by going to Appledore Island, Maine. This rugged, 39-ha island lies 16 km offshore in the southern Gulf of Maine. Treeless and bearing only 13 buildings, the island offers few natural nest sites for honey bees. And before conducting experiments, I further reduced the number of preexisting nest sites by establishing swarms on the island, reading the scouts' dances to locate the nest sites they had discovered (chimneys and cavities in walls of buildings) and then eliminating these nest sites by filling them and/or sealing off access to them.

Artificial Swarm Preparation. Swarms were prepared from six honey bee colonies transported to Appledore Island from Dyce Laboratory, Cornell University. To prepare an artificial swarm, I first shook the workers for the swarm off frames of a beehive into a swarm cage (15 × 25 × 25 cm) of wood with wire screen sides using a large wooden funnel. Then the swarm's queen was confined in a Benton mailing cage for queens (3.2 × 10 × 1.6 cm) which I suspended amidst the workers in the larger swarm cage. The bees were confined and fed liberally with a 50% sucrose solution for at least two days. Following this confinement the bees behaved like a natural swarm. They would not return to the parent hive, but would search for a new home site. To ensure that swarms consisted initially of inexperienced bees, ones not yet used in an experiment, I never returned swarms to the six source colonies, but instead put them in separate receiving hives.

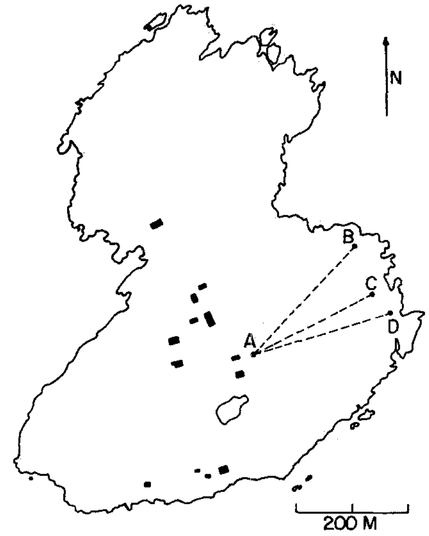


Fig. 3. Appledore Island, Maine. The experimental array consisted of the swarm site (*A*), an observation hut (*C*), and two matched sites (*B*, *D*) for nestboxes in choice experiments

I controlled swarm size by weighing the workers shaken into the swarm cage. Unless specified otherwise, swarms weighed approximately 2 kg (about 15,000 bees), a typical size for natural swarms (Burgett and Morse, 1974). In some experiments, recognition of certain individuals of the swarm was essential. Smaller, approximately 250-g swarms were prepared for these experiments. Then after the swarm was placed on a cross (see below), using eight colors of paint, I gave the bees of these small swarms individually distinctive paint marks by varying the color combinations and the forms of the paint marks.

Experimental Layout. The experimental array on Appledore Island is shown in Figure 3. Site A was the swarm site. I positioned swarms here on an upright wooden cross (120 cm high with a 46-cm-long cross member) by tying the caged queen to the cross and shaking the workers from the swarm cage at the foot of the cross. The workers would crawl up the cross and cluster around the caged queen. Each swarm was fed sugar syrup from a 1-l feeder jar.

Sites B and D were the nestbox locations in experiments involving a choice between two nestboxes. In choosing sites B and D, I sought two positions which were (1) equidistant from the swarm at site A, (2) separated by at least 30° for swarms at site A, and (3) matched in exposure to wind, sun and rain. Both sites were small, protected hollows, sheltered on two sides by granite outcroppings. I further equalized the nestbox exposures at sites B and D by placing at both sites identical shelters for the nestboxes as shown in Figure 5B.

Site C was the position of the observation hut used in the ethogram study and in the test of walking's importance to volume perception. This observation hut (122 × 122 × 183 cm tall) provided a small, dark chamber. The hut possessed lightproof joints, flat black inner walls, and a base sunk beneath ground level. Experimental nestboxes were mounted inside and outside the hut, on its walls. Windows into these nestboxes allowed observation inside them, while the hut's interior darkness helped minimize the artificiality of the nestboxes' window-walls.

Meteorological Records. Air temperature, wind velocity and barometric pressure were monitored with a Heathkit ID-1290 weather station.

b) Ethogram of Nest Site Inspection

The description of scout bee behavior during inspection of nest sites was an essential preliminary to the experimental analysis of the sensory mode(s) of

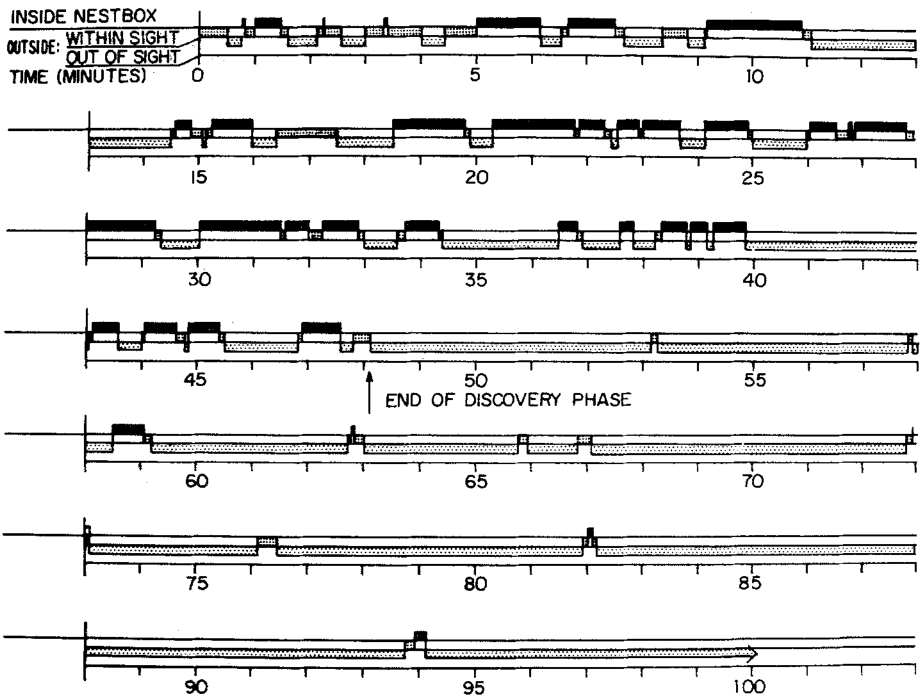


Fig. 4. Temporal and spatial record of one scout bee's inspection of a nestbox. The bee was followed for 100 min starting with her initial arrival at the nestbox. Her position was recorded as either inside the nestbox or outside, and when outside, as either within sight (near the nestbox) or out of sight (away from the nestbox). The discovery phase is the initial period of intense nest site inspection

volume perception. To assemble the complete ethogram, I needed to follow a scout's activities both inside and outside a nest cavity.

I accomplished this by mounting a cubical, 30-l nestbox outside the observation hut, against one of its walls. One wall of this nestbox was open, and this open side was aligned with a matching opening in the wall of the observation hut. A sheet of red No. 2423 Plexiglas, whose light-transmittance curve closely complements the honey bee's visual spectrum, provided a window-wall between the nestbox and observation hut. With this arrangement I could peer unseen inside the nestbox. Light entered the 3-cm diameter entrance hole centered in one wall of the nestbox and illuminated the nestbox interior. The inner walls, floor and ceiling of the nestbox were gridded into a total of 96 grid squares, each with a number in its center. With this grid system I generated temporal and spatial records of scout's movements inside the cavity by tape recording my oral reports of a scout's consecutive positions on the grids. Because I wanted complete records of individuals' inspection behaviors, small (250-g) swarms composed of marked individuals were used throughout the ethogram experiments. The procedure for these experiments was to prepare an artificial swarm early on day 1, confine the swarm through days 1 and 2, place the swarm on the cross and paint the bees on day 3, and finally uncork the nestbox entrance and start observations on day 4. Because it was impossible to follow a single scout both inside and outside the nest cavity, individual swarms were devoted exclusively to either inside or outside observations. Then later, a complete, typical ethogram of nest site inspection was assembled from both sets of observations.

Behavior Outside the Nest Cavity. Nest site inspection is a lengthy process. Figure 4 shows a typical scout's program of inspection over the 100 min following her initial arrival at the nest site. The most striking feature of this program is how, for the first 48 min, it consists of numerous, brief, interior inspections alternating with short periods outside the nest cavity. This initial phase in which a scout is primarily at the nest site, popping in and out of the nest cavity, I call the "discovery phase". Discovery phases vary considerably in duration ($\bar{X}=37$, $SD=15$, range 13–56 min; $N=10$). Following the discovery phase, a scout continues to visit the nest site, but the visits become sporadic and brief. Apparently during the discovery phase the scout inspects and evaluates a nest site. Then following the discovery phase she operates primarily away from the nest site, perhaps back at the swarm advertising the nest site, or perhaps off inspecting other nest sites.

The principal behaviors outside the nest cavity include extensive crawling about the outer surfaces of the nest structure, and slow, hovering flights all around the nest site. During these flights the scout orients with her head usually facing the nest structure. The scout appears to perform a detailed visual inspection of the nest site. The outside inspection concentrates first on the nest structure proper, and then is extended to objects – rocks, bushes, trees – increasingly distant from the nest structure.

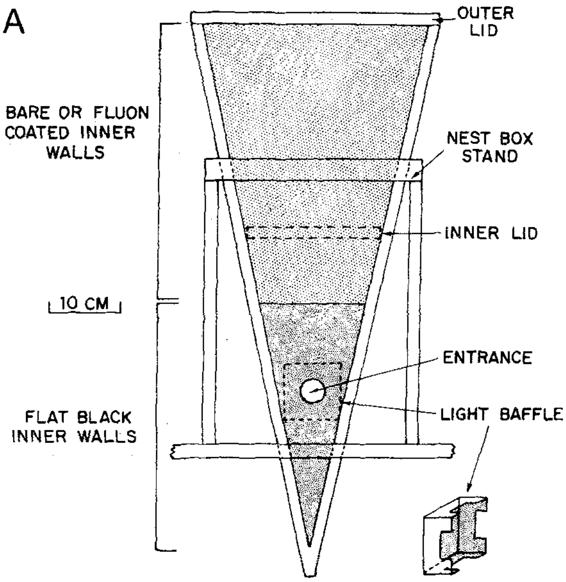
The authenticity of inspection behaviors observed with scouts from artificial swarms inspecting an experimental nestbox may be questioned. However, during the test of volume selection (Section 2) I observed the inspection behavior of many scouts under natural conditions, and I detected no qualitative differences in inspection behavior between the natural and experimental settings.

Behavior Inside the Nest Cavity. The principal interior behavior is rapid (5–7 cm/s) walking about a cavity's inner surfaces. Scouts devote roughly 70% of their interior time to this activity. This quick pacing is interspersed with brief flights, usually under 1 s, in which a scout hops from one point to another. Rarely, the flight lasts for several seconds as the scout hovers slowly about inside the cavity. Instances of grooming, resting, trophallaxis with other scouts and scenting (exposure of Nasanov gland plus wing-fanning) at the entrance further punctuate periods inside the cavity. An analysis of the patterns in scout movements inside cavities (Section 5.f.) follows the experimental demonstration of the significance of walking to volume perception.

c) Experiments with Deprivation of Sensory Input

In these experiments I sought to identify the sensory channels involved in volume perception by selectively eliminating potential modes of sensory input and then testing the bee's volume perception ability. The ethogram of nest site inspection suggested that inputs involving walking and vision might play a role in volume perception.

Nestboxes of the design shown in Figure 5 allowed independent modulation of the walking and illumination conditions inside a nestbox whose volume was also adjustable. The nestbox volume could be varied between two values, 5 or 25 l, by positioning the inner lid down or up, respectively.



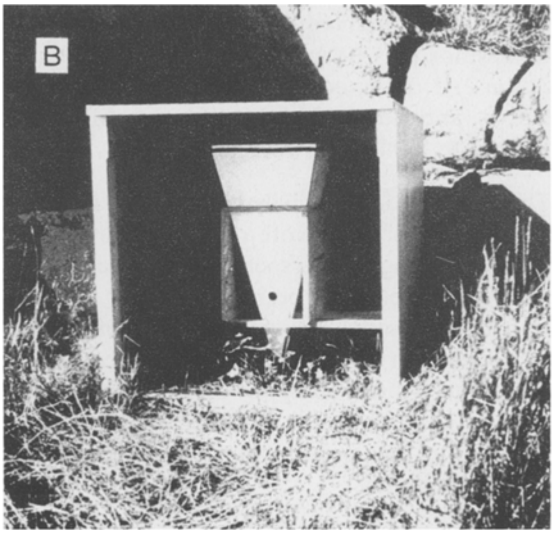


Fig. 5A and B. The design of nestboxes used in the sensory deprivation experiments. **A** Vertical cross-section and detail of light baffle. **B** Nestbox inside a nestbox shelter

The outer lid was sealed in place with opaque photographic tape. The pyramid form ensured an identical shape of the nest cavity at both volume settings. Interior illumination was modulated between approximately 150 lux and below 0.50 lux by positioning either a transparent or a flat black Plexiglas light baffle inside the entrance. Illumination levels were measured with a Gossen Super Pilot light meter whose sensitivity range is 0.52 to 350,000 lux. The light meter was fitted to a third pyramid nestbox, which, except for its light meter aperture, was identical to the two nestboxes offered to the bees. Light measurements were made using this third nestbox to avoid disrupting the process of nest site inspection.

The upper walls and ceilings of the nestboxes were either left as bare wood, or were coated with Fluon GP-1 (ICI America, Inc., Stamford, Conn.), a teflon-type material with a dry waxy texture. Bees cannot walk upside down across Fluon-coated surfaces or up Fluon-coated surfaces inclined at 77° from horizontal, the wall angle of the pyramid nestboxes. This was demonstrated by inclining a board at 77° inside the observation nestbox used in the ethogram study. Half of this inclined wall and half of the nestbox ceiling were coated with Fluon. Then the walking patterns of scouts inside the nestbox were observed as with the ethogram. Scouts crossed all the bare wood surfaces inside the nestbox, but could not traverse the Fluon-coated surfaces. Bees were not repelled from these surfaces. Rather, on coming upon the edge of a Fluon region, a scout would simply lose her grip on the Fluon, flail her sliding front legs for a moment, and finally withdraw back onto the grippable bare wood surface. Thus by coating the upper surfaces of the nestbox interior with Fluon, walking about the upper portion of the nestbox was prevented. In this way I could equalize the traversable wall area for both volume settings.

I measured the bees' preference between nestboxes by counting the number of bees visible at the nestboxes. High-quality sites are repeatedly visited and recruited to, and so acquire numerous scouts; lower-quality sites receive less attention from scouts (Lindauer, 1955). Each recorded value of the number of visible scouts represents the mean of ten counts, made at 15-s intervals, of the number of scouts visible from 2 m directly in front of the nestbox.

Bees were tested for volume perception by presenting them a choice between nestboxes set at 5 and 25 l. The two nestboxes were positioned at sites B and D. If the bees can distinguish the nestbox volumes, then they should prefer the site with the 25-l nestbox; but if they are unable to distinguish the volumes, then no preference or a preference independent of nestbox volume should appear. Control for nestbox position was by repeated reversal of the site with the 25-l nestbox. Control for the volume switch operation, which might frighten bees from one site to the other, involved a sham volume switch in each trial. That is, all the activities of a volume switch were performed – removing the nestbox from the nestbox shelter, unsealing the outer lid, moving the inner lid, resealing the outer lid and repositioning the nestbox – but without switching the nestbox volume.

A single series of experiments required six days. On day 1 a 2-kg swarm was placed on the cross at site A. Over the next five days of good weather the swarm was tested for volume perception with a different sensory environment inside the nestboxes each day.

Figure 6 shows the results from one series of input blockage experiments. A second series was also conducted. The outcomes were the same for both series.

Test A: Illuminated Interior, Bare Walls. In the first test, both relatively high interior illumination and completely traversable inner surfaces were provided. Volume perception was demonstrated by the bees' nest site preference which closely tracked the site whose nestbox was set at 25 l (Fig. 6A). The sham volume switch did not affect the nest site preference. Thus this first test demonstrates two things: (1) bees can measure cavity volume under the experimental conditions, and (2) perception of cavity volume does not rely upon information from the nest structure's exterior. The exterior appearances of the nestboxes were identical throughout the experiment.

Test B: Darkened Interior, Bare Walls. As is shown in Figure 6B, reducing the interior illumination to below 0.52 lux did not disrupt the bees' volume perception. Again the nest site preference closely tracked the location with the nestbox set at 25 l. Therefore this experiment demonstrates that cavity illumination above 0.52 lux is not always essential to volume perception.

Test C: Illuminated Interior, Fluon-coated Walls. Figure 6C shows that equalization of the traversable wall areas using Fluon did not make the nestboxes

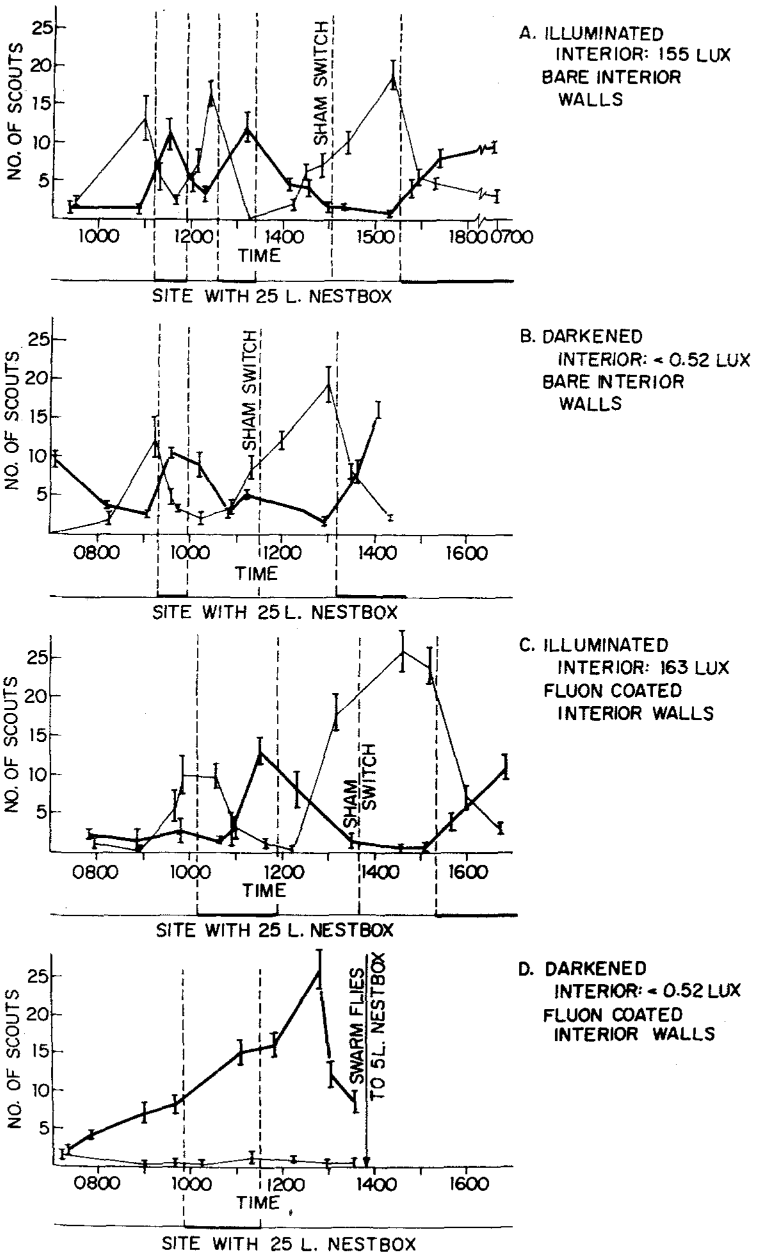


Fig. 6A–D. Tests of volume perception in various sensory environments. In all four tests (**A**, **B**, **C**, **D**) a swarm was given a choice between two nestboxes (design shown in Fig. 5), one set at 5 l, the other at 25 l. The two nestboxes were positioned at sites B and D (see Fig. 3). The swarm's preference between nestboxes was measured by counting the scouts at each nestbox. *Heavy lines* denote scout counts for the site B nestbox; *light lines* represent site D counts. *Vertical bars* give standard errors. The positions of the 5-l and 25-l nestboxes were repeatedly switched to control for site bias in the nestbox preference. *Lower abscissas* indicate the site at which the nestbox was set at 25 l (*heavy line*, site B; *light line*, site D) at each stage of the tests. Tracking of the site whose nestbox was set at 25 l with increases in the number of scouts (A, B, C) demonstrates volume discrimination. Nest site preference independent of nestbox volume (D) indicates failure of volume perception. Details in text

Table 2. Meteorological records for five days of sensory deprivation experiments

Date	Test	Air temperature (°C) Wind velocity (km/h–direction)						Barometric pressure (mm Hg)
		08.00	10.00	12.00	14.00	16.00	18.00	
28/July/76	A	17 5-WNW	21 11-NNW	25 13-NW	25 16-WNW	24 14-NW	22 16-NNW	760.9
29/July/76	B	18 0	21 3-NE	23 3-NE	21 3-NE	22 2-NE	21 3-ENE	764.3
2/Aug/76	C	18 6-NNW	20 2-WSW	24 3-SSE	22 8-SE	22 13-S	21 8-SSW	763.0
3/Aug/76	D	14 7-NNW	16 3-WNW	21 –	23 10-SE	23 13-SSE	22 11-S	769.9
4/Aug/76	E	17 3-WNW	19 3-SSW	21 5-S	21 10-S	20 10-S	18 11-SW	768.4

Test letters refer to letters given in text and in Figure 6

unacceptable and did not prevent the bees from discriminating nestbox volumes. Therefore completely traversable inner surfaces are not always essential for volume perception.

Test D: Darkened Interior, Fluon-coated Walls. In this experiment the nestbox interiors were darkened, their traversable wall areas were equalized, and the bees' nest site preference was unresponsive to changes in nestbox volume (Fig. 6D). Throughout the morning the scouts preferred the site B nestbox, regardless of its volume setting, and then in the afternoon the swarm flew to this nestbox, even though its volume for the past 2 h and 20 min had been only 5 l[2]. This outcome suggests failure to discriminate nestbox volumes.

Test E: Illuminated Interior, Bare Walls. The bees' insensitivity to nestbox volume in Test D could reflect either a general deterioration of the swarm or the inability to discriminate volumes. To distinguish these possibilities, the swarm was retested for volume perception under the conditions of Test A on the following day. The results were comparable to those shown in Figure 6A. Thus the swarm on the day of Test D was probably physiologically capable of distinguishing nestbox volumes.

In addition, the meterological records for the test days, Table 2, show nothing unusual for the day of Test D. All test days were sunny, hot and with light winds.

Therefore Test D, interpreted in context with the other tests, indicates that at least one of two conditions must exist for successful volume perception of nest cavities: (1) interior illumination above 0.52 lux, or (2) inner surfaces which can be completely traversed by walking.

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[2] The swarm did not remain at the nestbox, but promptly returned to its queen, still caged on the cross at site A

d) Test of Volume Perception by Form Vision

The honey bee's ability to measure the volumes of illuminated cavities whose interior surfaces offer only limited walking area (Section 5.c., Test C) suggests volume perception by form vision. That is, perhaps the scout simply enters, looks around, and so estimates the cavity size. To test this hypothesis I tried visual tricking of bees making volume measurements.

In procedure, the visual tricking experiments closely followed the preceding experiments. A 2-kg swarm was presented with a choice between two nestboxes, one each at sites B and D, and the swarm's nestbox preference was determined from the number of scouts visible at each nestbox. The two nestboxes were 25-l cubes built of 1.5-cm plywood and with a 3-cm diameter entrance hole in one corner. The nestbox interiors could be rearranged to produce the three interior arrangements shown in vertical cross-section in Figure 7A. The type-I arrangement consists of three sheets of No. 7058 glass (Corning Glass Works, Corning, New York) positioned in the entrance corner. This glass transmits approximately 90% of light with wavelengths from 300 to 2500 nm and so should appear clear to honey bees. Thus the type-I arrangement reduces the accessible nestbox to a cubical, 4.3-l space, but does so with transparent walls. The type-II arrangement also reduces the accessible nestbox space to a 4.3-l cube, but does so with opaque wooden walls. And thirdly, the type-III arrangement uses no inner walls and therefore maintains the fundamental nestbox volume of 25 l. To equalize the appearance and texture of the inner surfaces in all three arrangements, plate glass liners of the ceiling and the two walls opposite the entrance corner were positioned in the nestboxes as shown in Figure 7A. To equalize nestbox odor for the three arrangements, the various inner wall components were stacked in one corner of the nestbox when not in use and so were never removed from the nestboxes.

To summarize the three possible nestbox interiors shown in Figure 7A, arrangement I produces a 4.3-l nest cavity which might appear 25 l in volume; arrangement II gives a 4.3-l nest cavity which can only appear 4.3 l in volume, and arrangement III offers a 25-l nest cavity which can only appear 25 l in volume.

The outcomes of the choice experiments, shown in Figure 7B, appear conclusive. The bees were not tricked into adopting a nestbox with a type-I arrangement. Instead, both arrangements I and II, with 4.3-l volumes, were uniformly rejected, while only the 25-l arrangement III was ever accepted. The rejection of arrangement I has two explanations. Either the bees do not use form vision for volume perception, or they do use form vision, but were not tricked here because they saw the transparent walls, or because the volume perception based on form vision was overridden by a volume perception based on other inputs. In short, the outcome neither proves nor disproves volume perception by form vision.

e) The Importance of Walking to Volume Perception

Two observations suggest that walking about a cavity's inner surfaces might be involved in volume perception: (1) the extensive walking by scouts inspecting a cavity interior (Section 5.b.), and (2) the bee's ability to discriminate volumes of cavities with traversable inner surfaces and low (<0.52 lux) interior illumina-

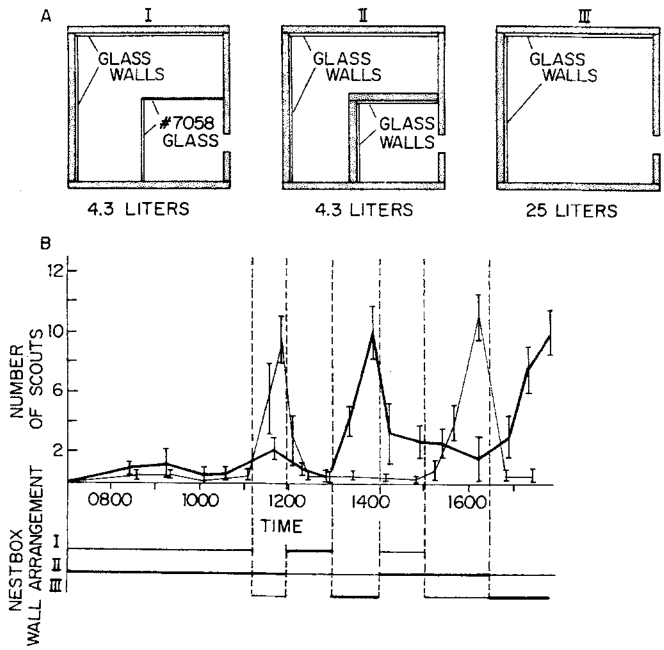

Fig. 7A and B. Experiment in visual tricking of bees making volume measurements of nest cavities. A swarm was given a choice between two nestboxes, one each at sides B and D (see Fig. 3), whose inner walls could be given the three arrangements shown in **A**. Arrangement I created a nest cavity which was unsuitably small (4.3 l), but which might appear to scout bees to be suitably large (25 l). Arrangements II and III created cavities which were and would appear unsuitably small (4.3 l) and suitably large (25 l), respectively. Acceptance of a nestbox with a type-I wall arrangement would demonstrate visual tricking and imply visual input in volume perception. **B** Nest site preference as a function of nestbox wall arrangement. The swarm's preference between the two nestboxes was measured by counting the scouts at each nestbox. *Heavy line* denotes scout counts for the site B nestbox; *light line* represents site D counts. *Vertical bars* give standard errors. *Lower abscissas* indicate the wall arrangements in the two nestboxes at each stage of the test. Only nestboxes given type III wall arrangements were strongly preferred. Thus visual tricking of bees making volume measurements did not occur

tion (Section 5.d.). Vision is probably limited at this illumination level. The threshold illuminations for honey bee optomotor response are 2 lux and 0.26 lux following 10 s and 300 s, respectively, of dark adaptation (Autrum and Seibt, 1965). Also, the first flights to a nearby, attractive feeding place require 1.5–5.0 lux illumination (Lindauer and Schricker, 1963). However, Schricker (1965) reports foraging can start when the light outside the nest is still under 1.0 lux.

To test the role of walking in volume perception, I tried manipulating scout bees' volume perceptions by varying the amount of walking required to move from point to point inside a nest cavity. I modulated walking distances using the nestbox diagrammed in Figure 8. This nestbox provided a nest cavity with manually rotatable walls, but a stationary entrance. With this apparatus I could force a scout to walk longer or shorther horizontal distances in moving from

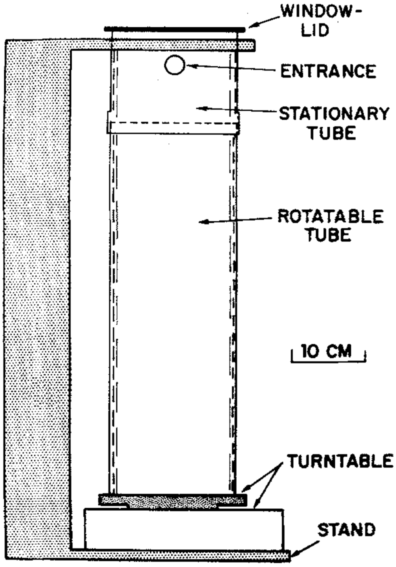

Fig. 8. The rotatable wall nestbox used in testing the importance of walking to volume perception

one point to another inside the nestbox than would have been necessary in a fixed wall nestbox of the same design. To make a bee walk more or less than normally, I rotated the walls in either the opposite or the same direction, respectively, as the scout's own horizontal component of walking direction.

The logic of the experiments is as follows. The volume of the rotatable wall nestbox is 14.3 l. Thus its volume is on the boundary between unacceptably small and suitably large nest cavities (see Fig. 1). Therefore, any modification in a scout's perception of the nestbox volume should make the nestbox seem either more or less attractive than its true volume would merit. This divergence in evaluation should allow monitoring of differences in volume perception. For a scout which concludes that the site is suitably large should recruit more scouts to the site than a scout which perceives the nestbox as unacceptably small.

The rotatable wall nestbox was mounted inside the observation hut at site C. A 20-cm length of 2.5-cm O.D. Tygon tubing connected the nestbox entrance with an entrance hole in the observation hut's wall. The only light entering the nestbox came through this entrance. The interior illumination therefore was low, approximately 8 lux, but sufficient for observing moving bees against the nestbox's white walls. A clear Plexiglas lid allowed viewing inside the nestbox. The Tygon entrance tube was well illuminated and individually marked bees could be recognized while traversing this tube. Observations during experiments were spoken and tape recorded.

Each trial required two days. On the morning of day 1 the nestbox entrance was plugged, a 0.25-kg swarm was placed on a wooden cross 10 m north of the observation hut, and the bees were marked for individual recognition. By early afternoon the marking was completed and the swarm was transferred from the cross into an empty beehive. During the night I carried the swarm and beehive to site A. At 09.00 on day 2, the swarm was placed on the site A cross. This series of operations produced a small swarm, composed of recognizable individuals which was trained to house hunt near site C.

Table 3. Meteorological conditions and results of test for change in volume perception by manipulating walking behavior inside a cavity

Date	Air temperature (°C) Wind velocity (km/h–direction) Barometric pressure (mm Hg)					Test period	Treatment of first scout	Number of arrivals
Time	08.00	10.00	12.00	14.00	16.00			
26/Aug/76	16.8 0 759.2	20.2 5-SSW 759.5	19.6 8-SSE 759.7	21.3 10-S 759.2	17.9 16-SW 758.4	12:37–14:07	+	9
29/Aug/76	14.6 5-SSW 757.7	18.5 5-SSW 757.9	21.3 3-WSW 757.9	21.3 11-SE 757.9	19.6 11-SE 757.7	13:04–14:34	–	0
8/Sept/76	13.4 10-NW 764.3	16.2 3-NNW 764.8	22.4 14-E 765.0	17.4 14-E 765.1	15.1 11-SE 765.3	13:23–14:53	–	2
10/Sept/76	11.2 2-NW 774.1	12.9 3-NNE 768.6	17.9 6-ESE 774.1	19.6 6-SE 767.1	20.7 8-ESE 766.6	12:41–14:11	+	7

Increased walking is denoted by “ + ”, decreased by “ – ”. Details in text

The real experiment started at 12.00 on day 2 when I uncorked the entrance hole to the rotatable wall nestbox. Within two hours the first scout would discover the nestbox entrance and enter. This first scout was the sole bee in each trial whose volume perception I attempted to manipulate. Subsequent scouts were noted upon arrival, but otherwise were ignored while controlling the nestbox wall rotation to match or counter the first scout's walking direction. When matching the walking direction, I roughly halved the horizontal movement needed to walk between points; when countering, I approximately doubled the horizontal movement required. These two operations of manipulating the first scout's walking, and recording arrivals of other scouts, were continued for 90 min following the moment the first scout entered the nestbox.

Table 3 compares the data from four trials of this experiment. The data appear conclusive. In the two trials in which the first scout was forced to walk greater than normal horizontal distances, significantly more bees arrived in the 90-min recording period than when the scout was forced to walk less than normal horizontal distances ($P < 0.05$, Student's t test, single-tailed distributions). By the reasoning delineated above, this outcome implies that differences in scouts' volume perceptions resulted from varying the amount of walking required to move from point inside the nest cavity. Thus the extensive walking by scouts about a cavity's inner surfaces plays a role in measuring the cavity's volume. Apparently a volume perception is a positive function of the amount of walking needed to subtend portions of a cavity's perimeter.

f) Spatial Patterns of Movement Inside a Cavity

A detailed spatial analysis of one scout bee's movements throughout a cavity inspection is now in order. The data for this analysis were collected while

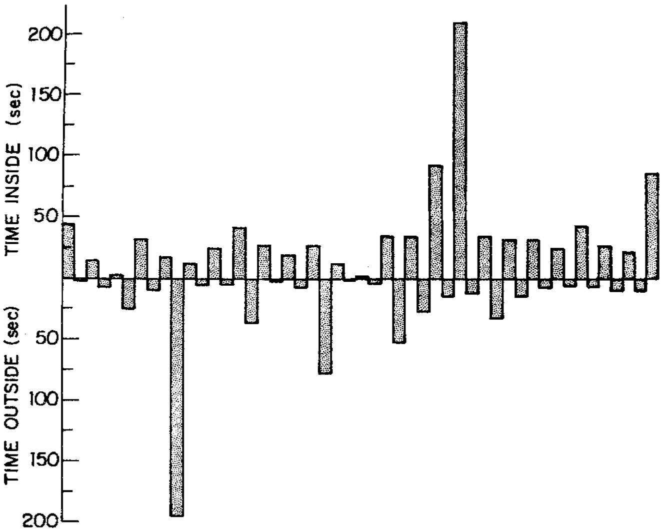

Fig. 9. The durations of the 25 inside and the 24 outside insections of a nest cavity throughout one scout's discovery phase

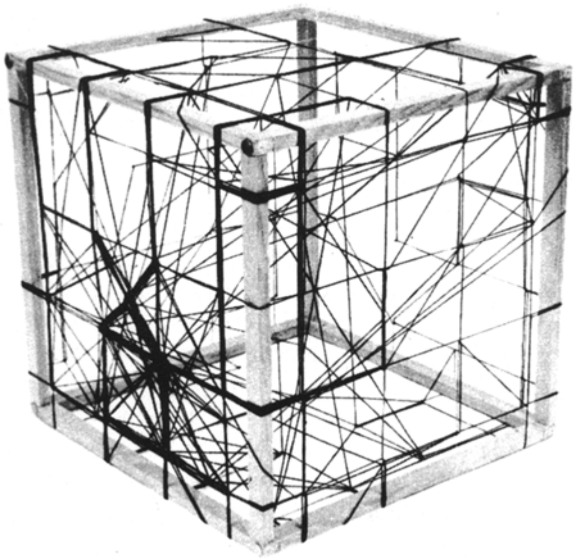

Fig. 10. Three-dimensional reconstruction of the total movement pattern generated by a scout during her interior inspections of a cubical nestbox. *All black lines* denote movement paths. Pathways are simplified to *straight lines* because the resolution of pathway recording permitted only approximate path plots. The entrance was centered in the left front side as is indicated by the high path density in this area

assembling the ethogram of nest site inspection. The movement patterns generated by the one scout considered here are probably typical. Identical analyses of three other scouts' movements revealed similar patterns.

Figure 9 shows the durations of the 25 inside and the 24 outside inspections of the nestbox which comprised the scout's discovery phase. Inspection time was partitioned into time inside (63%) and time outside (37%), with mean inspection durations of 38.4 s and 23.9 s, respectively. This figure emphasizes the rough balance between inside and outside inspections and how the discovery phase is composed of many brief and alternating interior and exterior inspections.

Figure 10 is a three-dimensional reconstruction of the total movement pattern generated by the scout during her interior inspections of the nestbox. Black diagonal lines through the cube's interior denote flight paths; black lines across the cube's surface represent walking paths. All pathways are somewhat simplified here because the resolution of pathway recording permitted only approximate path plots. However, the model accurately shows the solidity of inner surface coverage produced by the scout's walking and flying inside the cavity. The particularly high path density around the entrance underscores the pattern of repeated entries and exits during the discovery phase. The total distance of the scout's inside movements, measured as the length of string used in constructing the Figure 10 model, was 63.1 m. However, because this model simplifies highly convoluted movements (see Fig. 11) to straight lines, the actual movement distance was somewhat greater than 63.1 m.

Figure 11 shows the detailed movement patterns from three of the scout's visits inside the nestbox. The paths are quite convoluted. The scout rarely retraced her steps as would occur if she were orienting by chemical trails.

In the search for spatial patterns in the inspection movements, comparisons were made between visits of the distance and direction of movements within visits. Figure 12 presents the analysis of movement direction for all 25 interior visits. Directions are relative to the nestbox entrance. The surface of the nestbox interior was partitioned into an octet of directional regions, as shown in the first "exploded" nestbox of Figure 12. In the following "exploded" nestboxes, the bar lengths represent the fraction of the total entries into grid squares (shown in Fig. 13B) during each visit made into the grid squares of the corresponding directional region. Entries into grid squares bisected by a boundary between two directional regions were counted as one half an entry for the two adjacent regions. The pattern of movement direction is clear. During a single visit inside, the scout moves mostly within half or fewer of the directional regions. Thus for each visit, movement tends to occur in a general direction from the entrance. Moreover, sequential visits generally show different directions of movement; but there seems to be no pattern in the series of movement directions over several sequential visits.

The pattern of movement away from the entrance was revealed by dividing the inner surface of the nestbox into four areas approximately concentric about the entrance (Fig. 12B). The 25 visits were grouped into five sets for averaging. Then for each quintet of visits, the fraction of the total entries into grid squares was calculated for each of the four concentric regions. Figure 13A shows the pattern generated. In early visits the scout moved about mostly near the entrance,

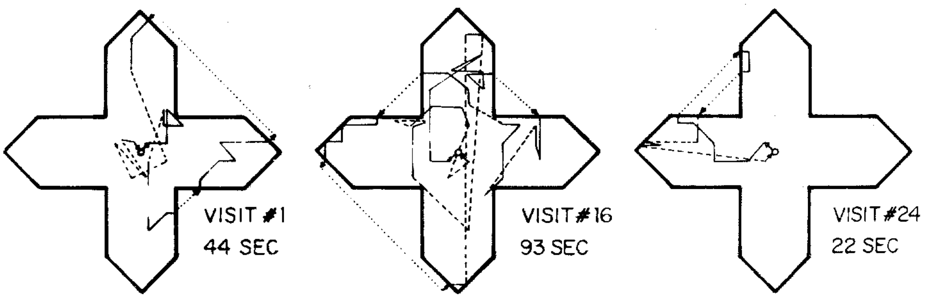

Fig. 11. Detailed movement patterns inside a nestbox for three separate interior visits by the same scout. To simplify the representations, the nestbox was "exploded" onto two dimensions. The entrance is at the center. *Solid lines* denote walking paths, *dashed lines* represent flight paths. *Dotted lines* are artificial connectives created by the 3-D to 2-D conversion

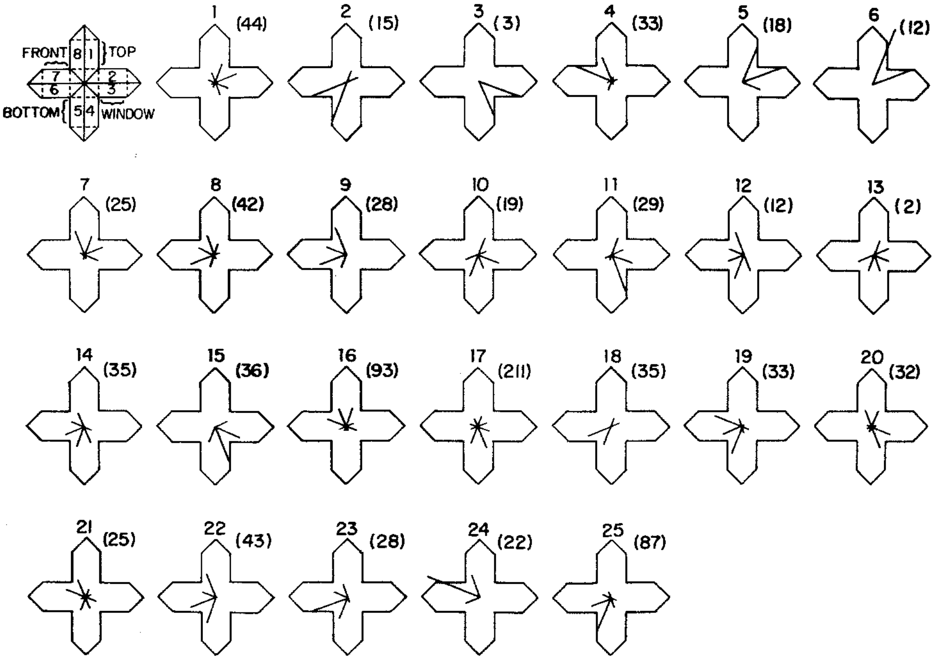

Fig. 12. The patterns of movement directions, relative to the entrance, for the 25 interior inspections of one scout's discovery phase. The nestbox has been "exploded" onto two dimensions with the entrance at the center as in Figure 11. *Bar length* denotes intensity of movement in the corresponding directional region. Duration of visit, in seconds, is noted *in parentheses* for each visit

but with later visits the movements became increasingly distributed over more distant regions of the nestbox interior.

In summary, the interior inspection of a nest cavity is composed of numerous brief visits. One result of these visits is that a scout traverses most of the cavity's internal surfaces through a combination of short flights and highly winding walks. However, during individual visits inside, a scout does not cover the entire cavity interior, but moves about in a general direction from the entrance. With later visits, regions of the cavity more distant from the entrance are increasingly inspected.

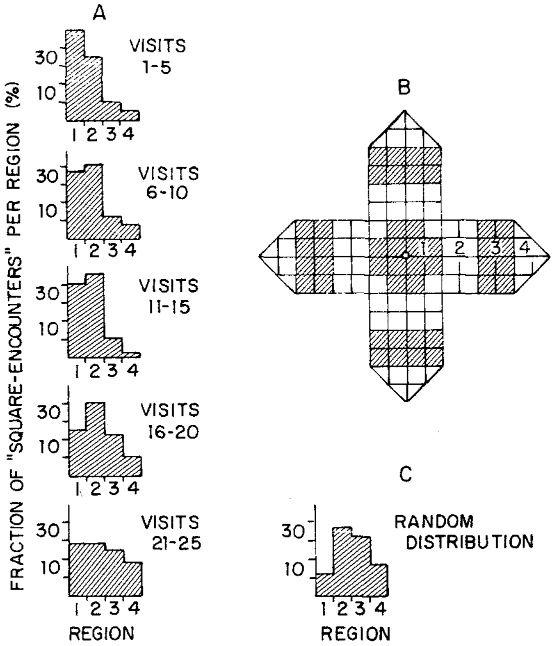

Fig. 13A–C. Pattern of movement away from the entrance. **A** Distributions of activity in the four concentric regions shown in **B** with averaging over five visits. **C** The reference distribution for uniform activity about the interior surfaces. Inter-regional differences in **C** reflect differences in region sizes

6. *Natural Conditions for Volume Perception*

a) Volume Distribution of Natural Cavities

The outcome of a choice is always limited by the set of available alternatives. Therefore, to understand fully the origins of the volume distribution of natural nests (Fig. 1), one must both understand the honey bee's volume preference and know the setting in which this preference operates: the volume distribution of natural cavities.

A volume distribution for tree cavities was obtained by clearing a 3250 m^2 area of hillside in Roxbury, Vermont. The woods of this area are maple (*Acer*) and beech (*Fugus*) forests which had been logged in the 19th century. These woods are quite similar to those around Ithaca, New York, where I collected the bee trees for the volume distribution of natural nests. We only felled trees with diameters above 20 cm as measured 1 m off the ground. To reveal cavities inside these trees, each tree was sawed into approximately 120 cm lengths. Sections containing cavities were further split in half. Then the volume of the exposed cavity was roughly calculated from measurements of the cavity length and of the cavity diameter made every 20 cm down the length of the cavity.

Fourteen cavities were found in 39 felled trees. The volume distribution is shown in Figure 14, together with the volume distribution curve for natural nests. If both distributions generally hold true, then they imply that the bee's

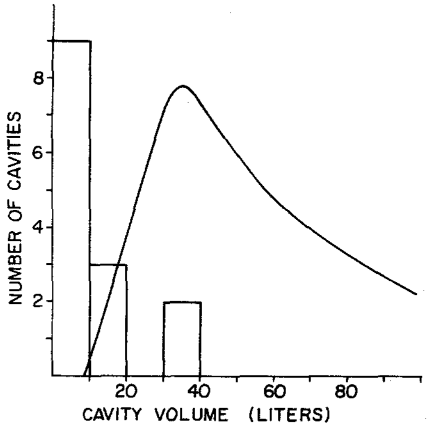

Fig. 14. Volume distribution for tree cavities (histogram). *Curve* is the corresponding portion of the distribution curve of natural nest volumes from Figure 1

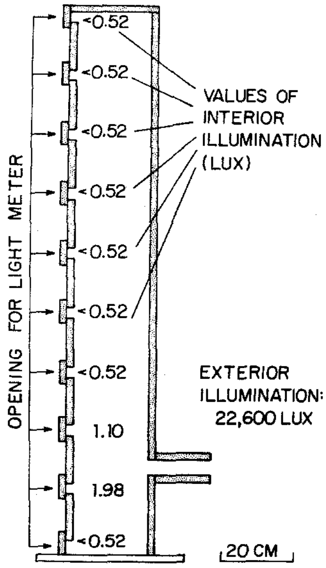

Fig. 15. Model of natural cavities used in estimating the typical illumination conditions inside natural cavities

most frequent exercise of its volume perception powers is in rejecting cavities which are too small to serve as nest cavities, whereas excessively large cavities are relatively rarely encountered.

b) Illumination Inside a Model Tree Cavity

The experiments on the mechanism of volume perception demonstrate that two mechanisms exist, one which utilizes walking about inside the cavity, and a second which does not require such pacing but does need cavity illumination above 0.52 lux.

To evaluate the relative importance of the two volume perception mechanisms under natural conditions, I estimated the typical illumination conditions inside natural cavities using a model nest cavity. The model cavity's design was based on findings from the study of natural bee nests by Seeley and Morse (1976). Shown in Figure 15, the model cavity incorporates typical values of relevant variables of natural nests: height, 150 cm; horizontal cross-section area, 400 cm^2; entrance area, 16 cm^2; entrance in the bottom third of the nest; and 15 cm separating the entrance's outside aperture from the main cavity. Also, the model cavity's inner walls were stained dark brown to simulate the color of the decayed wood which lines tree cavities. Illumination was measured with a Gossen Super Pilot light meter which could be inserted in the nest cavity at several levels.

Values of interior illumination, shown in Figure 15, were very low. Most of the cavity was illuminated below 0.52 lux. If this is generally the case in nature, then this implies that the volume perception mechanism involving walking inside cavities is the primary means of honey bee volume perception.

Discussion

The full understanding of honey bee control of nest volume requires answers to three remaining questions. The first concerns the mechanism of volume perception. The present study demonstrates the importance of walking inside cavities to perception of their volume, but both the sensory inputs generated by this walking and how such inputs are reduced to a volume perception remain unspecified. One hypothesis is that a bee performs a form of vector calculus in which walking distances and directions are measured and then these vectorial data are integrated to a value for the cavity's volume. Distances might be measured using kinesthetic inputs from walking movements, energy expenditure in walking, or, as in the desert ant *Cataglyphis bicolor* (Duelli, 1976), duration of movement. Perception of movement directions could involve the gravitational sense organs (Lindauer and Nedel, 1959) to measure the vertical component, and the bright patch of light from the cavity's entrance as a reference for measuring horizontal components, just as flight angles are measured through reference to the sun.

Earlier experiments suggest that the integration operations invoked by the vector calculus hypothesis are within the honey bee's range of capacities. Numerous detour experiments (von Frisch, 1948, 1967; Heran and Lindauer, 1963; Lindauer, 1963) in which bees were forced to fly indirect, angular routes between hives and food sources have demonstrated that bees can calculate the angle of dancing corresponding to the direct air line between hive and food source. This involves the integration of solar angles and lengths of different flight segments. Also Bisetzky (1957) showed that bees forced to walk angular routes between their hive and food source can also perform the operations of measuring solar angles, quantifying movement distances and calculating the direct line between hive and food source.

The second major question is the function of the volume selection. The adaptiveness of avoiding small cavities appears clear. For in proximate terms, small (<20-l) cavities probably cannot enclose the combs, food and bees needed for a viable colony. Or in terms of ultimate causation, over evolutionary time the colony requirements of defense, labor and homeostasis may have fixed a lower limit on honey bee colony size. In understanding the avoidance of large (>100-l) cavities, an important clue may be Simpson's (1969) observation that the average colony of European *Apis mellifera*, when given unlimited hive space, will grow to fill 126 l of hive space. Thus in avoiding large cavities, honey bees impose a limit on their mature colony size considerably below their growth potential. It remains unproven whether colonies occupying intermediate-sized nests (20 to 100 l) are more fit than colonies in large nests (>100 l). However, given equal growth rates, small colonies will exhibit shorter generation times than large colonies. And Simpson (1973) has found that colonies limited to 37 l of hive space produce queens more rapidly than colonies given unlimited hive space. Thus the function of volume selection in nest cavities may be to regulate mature colony size at an optimum between small colonies with low survivorship and large colonies with low fertility.

The third major puzzle is the evolution of the volume selection process. When did it arise? Certainly not before the origin of the cavity nesting honey bees, *Apis mellifera* and *A. cerana*. The more ancestral honey bees, *A. florea* and *A. dorsata*, build exposed nests on the undersides of branches and so lack the need for this sensory capacity. The absence of volume selection by *A. cerana* would suggest that the behavior arose sometime after the speciation of *A. mellifora* and *A. cerana*. A second evolutionary question is the origin of the sensory and mental processes involved in volume perception. Solid statements on this must await deeper analysis of the mechanisms. However, if the vector calculus hypothesis proves correct, then the evolution of honey bee volume perception apparently consisted of combining preexisting sensory and orientation abilities in a new context to generate a new sensory capacity.

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