

**NEST SITE SELECTION
BY THE HONEY BEE, *APIS MELLIFERA***

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SUMMARY

1. Honey bees exhibit preferences in several nest site properties. The following preferences were identified (« > » means « preferred to ») : nest height, $5 > 1$ m; entrance area, $12.5 > 75$ cm²; entrance position, bottom > top of nest cavity, entrance direction, southward > northward; nest cavity volume, $10 < 40 > 100$ liters.

2. The data also suggest preferences exist for previously inhabited nest cavities and for nest sites beyond 300 m from the parent colony.

3. Nest sites with high exposure and visibility were occupied more rapidly than sites with low exposure and visibility. However, this difference probably reflects differential ease of nest site discovery rather than a preference for exposed nest sites.

4. No preferences were found in the following variables : entrance shape (slit vs. circle), nest cavity shape (cube vs. tall parallelepiped), cavity draftiness (sound vs. drafty), and cavity dryness (wet vs. dry). Cavity draftiness and dryness are probably important to bees, but because bees can seal and waterproof their nests, they may be less demanding about these two nest site variables than about those they cannot modify.

5. The complex process of nest site selection apparently benefits a honey bee colony in several ways, including facilitation of colony defense and hygiene, simplification of nest construction and microclimate control, and reduction of foraging competition with the parent colony.

ZUSAMMENFASSUNG

Kriterien für die Nestwahl bei der Honigbiene, *Apis mellifera*.

1. Honigbienen bevorzugen bestimmte Nistplatzeigenschaften. Die folgenden Bevorzugungen wurden herausgefunden (« > » bedeutet « bevorzugt gegenüber ») : Höhe des Nestes, $5 > 1$ m; Fläche des Eingangs, $12,5 > 75$ cm²; Lage des Eingangs,

Boden > Spitze; Richtung des Eingangs, nach Süden > nach Norden; Raum der Nesthöhle, 10 < 40 > 100 Liter.

2. Die Daten deuten darüber hinaus an, dass Honigbienen Nesthöhlen bevorzugen, die vorher bewohnt waren, oder die weiter als 300 m vom Mutterstock entfernt sind.

3. Exponierte und gut sichtbare Nistplätze werden schneller bezogen als weniger exponierte und weniger gut sichtbare Plätze. Wahrscheinlich hat dies aber seinen Grund darin, dass diese Plätze leichter entdeckt werden, nicht weil sie echt bevorzugt werden.

4. Keine Bevorzugung wurde für die folgenden Variablen gefunden: Form des Eingangs (Schlitz vs. Kreis), Form der Nesthöhle (Quader vs. hohe Rechtecksäule), Zugigkeit der Höhle (zugfrei vs. zugig) und Trockenheit (feucht vs. trocken). Wahrscheinlich sind Zugigkeit und Trockenheit der Höhle für die Biene wichtig. Da die Bienen jedoch ihr Nest abdichten und wasserdicht machen können, sind sie — was diese Nistplatz-Variablen angeht — nicht so wählerisch als gegenüber jenen, die sie nicht ändern können.

5. Dieser komplexe Prozess der Nistplatzwahl kommt der Honigbiene offensichtlich in verschiedener Weise zugute, z. B. zur Erleichterung der Verteidigung und Hygiene des Stockes, der Vereinfachung beim Nestbau und bei der Kontrolle des Mikroklimas, sowie zur Minderung der Futterkonkurrenz mit dem Muttervolk.

INTRODUCTION

Honey bee architecture has a long history of study, from analyses by eighteenth century geometers of the efficiency of honey comb form (reviewed by THOMPSON, 1942), through DARWIN'S (1859) studies of comb construction and the evolution of animal instinct, to more recent studies on the sensory physiology and behavior involved in nest construction (reviewed by DARCHEN, 1968 and von FRISCH, 1974). However, one aspect of honey bee nest building — selection of the nest site — has always received little attention. LINDAUER'S (1955) seminal study of home site selection, SEELEY'S (1977) analysis of the preferred nest cavity volume, and scattered observations in the beekeeping literature on trapping wild swarms, comprise our knowledge of nest site selection by honey bees. In this paper we review the previous findings and report further studies on the honey bee's preferences in nest site variables.

MATERIALS AND METHODS

Study area and bee races. — The study was conducted during the summers of 1975, 1976 and 1977 in the region of Ithaca, New York. We used wild swarms of honey bees in all the experiments, except for the study of the distance between old and new nests. Most of the wild swarms came from feral colonies which flourish in the Ithaca area, and the remainder came from unidentified beekeepers' colonies. In the study of swarm dispersal distance we used artificial swarms (MORSE, 1963; SEELEY, 1977) prepared from colonies of Dyce Laboratory, Cornell University. The honey bees in the Ithaca area are hybrids

of several bee races : *Apis mellifera ligustica* Spinola, *A. m. caucasica* Gorbatschew, *A. m. carnica* Pollman and *A. m. mellifera* L. (RUTTNER, 1975), Voucher specimens from 18 of the 52 wild swarms inhabiting the experimental nestboxes in 1977 were deposited in the Cornell University entomology collections (Cornell Univ. Lot n° 1067).

General experimental procedure. — All nest site properties, except for (1) distance between old and new nests and (2) nest site exposure, whose study techniques are described separately below, were studied using one basic system of materials and methods. This consisted of setting out nestboxes in pairs, called « nestbox stations », with the two nestboxes of a nestbox station differing in one variable. Wild swarms would discover the nestbox stations and inhabit one of the two nestboxes in a station. Finally the patterns of nestbox occupations were statistically analyzed by considering the swarms' selections between paired nestboxes as binomial processes. Some details of nestbox design and placement differed between experiments, and these will be noted with the descriptions of the individual experiments. However, many features of nestbox design and nestbox stations were the same for most or all experiments, and will now be described.

Nestbox design. — Nestboxes were constructed of 1.5 cm thick plywood and painted dark green on the outside. With a few exceptions noted below, the nestboxes were cube-shaped and had a 3 cm diameter entrance hole positioned midway across the front, 8 cm up from the nestbox floor. A nail driven horizontally across the entrance prevented occupation by birds. All nestboxes were 40 liters in volume. Nestbox floors were removable to permit interior inspections. A 4 × 4 cm piece of old bee 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.

Nestbox stations. — Nestboxes were set out in pairs, hereafter referred to as « nestbox stations », by nailing two nestboxes to trees along a hedgerow or to adjacent power line poles. To establish a nestbox station we first chose two sites which we judged were approximately equivalent in visibility, exposure and height, and which were 10 to 25 m apart. In all nestbox stations the nest sites were highly visible and were at least 3 m off the ground. The two nestboxes comprising a station were randomly assigned to the two nest sites in a station by flipping a coin. Both nestboxes in each station were positioned at the same height and with their entrances facing the same direction.

We inspected the nestbox stations approximately every 10 days throughout the two annual swarming periods for the Ithaca area, May 15 to July 15, and August 15 to September 15 (FELL *et al.*, 1977). Whenever a nestbox was occupied, we checked the inside of the other nestbox in the same station for ants, wasps and other sources of interference.

A control experiment described previously (SEELEY, 1977) showed that two nestboxes in a nestbox station which are at the same height and have the

same visibility will both be found by bees before they choose between them. Thus, except in the test of nest site exposure which used nestboxes set out singly instead of in pairs, and in the test of nest height which used nestboxes at different heights, the different occupation rates between nestboxes in a given experiment could not reflect differences in the ease of nestbox discovery.

Distance from parent nest. — To measure the distances which swarms travel between parent nests and new nest sites, we transported artificial swarms to Mount Pleasant, a large, heavily forested area near Ithaca, New York. Each swarm was placed on a wooden cross in a clearing surrounded by forest for at least 1 km and generally 2 or more km. Thus the swarms were surrounded for large distances by a presumably random distribution of natural nest sites. We followed each swarm's selection of a nest site by reading the scouts' dances to determine the distances and directions of the home sites they had discovered. The calibration curves of LINDAUER (1961) and von FRISCH (1967) for *Apis mellifera ligustica* were used to translate dance tempos into distances to the advertised nest sites. By watching the scouts' dances throughout a swarm's selection of a home site, we could determine the approximate distance to the nest site finally selected by each swarm.

Nest site exposure-visibility. — To test the importance of this variable, we set out twenty nestboxes of the design described above singly in a random pattern about the Ellis Hollow valley near Ithaca, New York. All nestboxes were 4 m off-ground. Ten nestboxes were located in sites with high exposure and visibility, such as on a telephone pole or on the side of a large tree in a hedgerow. The other ten nestboxes were positioned in sites with low exposure and visibility by nailing them to trees thickly surrounded by other trees. The two nestbox groups had the same distribution of nestbox entrance directions. We monitored these individual nestboxes just like the nestbox stations.

Statistical tests. — For most experiments the statistical test involved calculating the binomial probability of obtaining the observed pattern of occupation for the two nestbox types, or one even more skewed, assuming that both nestboxes in a station had equal probabilities of being inhabited by a swarm. For some of the experiments involving paired nestboxes, an *a priori* hypothesis about the direction of preference between nestboxes was formed based on observations of natural nests (SEELEY and MORSE, 1976). For these experiments onesided null hypotheses and significance tests were used. In all the other experiments using paired nestboxes, two-sided hypotheses and significance tests were employed. In the experiment on nest site exposure-visibility, we used the χ^2 -test, uncorrected and with Yates correction. Differences in the probability of nestbox occupation for nestboxes with different entrance directions were tested for significance using the MOSTELLOR, ROURKE and THOMAS (1973, p. 444) test for small samples. Differences in nestbox occupation probabilities between individual directional groups (compass octants) and the entire sample of directional groups were tested for significance using Student's t-test.

Curve fitting in fig. 1 and 2 was accomplished by locally fitting least-squares polynomials, up to quartics, to sets of three, five or seven equally spaced data points and then using the value of the fitted polynomial as the value of the probability density function at the middle point (HAMMING, 1973). End values of the functions for swarm flight distance were fitted by eye.

RESULTS

1. — Nest location.

a) Height.

The significance of nest height was tested by establishing nestbox stations with one nestbox 1 m, the other 5 m off-ground. Eight stations were established and 6 swarms inhabited high (5 m) nestboxes. One low (1 m) nestbox was also inhabited, but this followed a swarm's occupation of the high nestbox in the same station. Thus the high nest sites were more rapidly occupied than low sites ($p < 0.04$, two-tailed probability). Either bees prefer high nest sites or they have difficulty in finding low nest sites. The latter possibility seems improbable since whenever we observed scouts inspecting a high nestbox, we also saw scouts examining the low nestbox in the same station ($n = 5$ stations).

The apparent preference for high nest sites is consistent with the recommendation of beekeepers that bait hives (hives for trapping wild swarms of honey bees) are best located high off the ground (CAILLAS, 1946; MARTY, 1949; MARCHAND, 1967; GUY, 1971). Also, in medieval Europe (GALTON, 1971) and still currently in Africa (SMITH, 1960; TOWNSEND, 1970; ROBERTS, 1971; BROKENSHA *et al.*, 1972; REA, 1974), primitive beekeeping has relied upon placing uninhabited hives high in trees to catch swarms. Presumably improved defense makes high nest sites more attractive to bees than low ones.

b) Exposure-visibility.

Nest sites which are highly exposed to wind, sun and rain — such as hollow trees in clearings or along the edge of a forest — also tend to be quite visible. Inversely, a low exposure nest site — a hollow tree surrounded by forest — is generally a low visibility site. Thus the variables of nest site exposure and visibility are usually coupled in nature, and were likewise coupled in our experiment.

During one summer, 8 of the 10 high exposure-visibility nestboxes and 2 of the 10 low exposure-visibility nestboxes were inhabited by swarms. This demonstrates a significantly higher probability of swarm occupation for nestboxes with high rather than low exposure-visibility ($p < 0.01$, $\chi^2 = 7.2$ uncorrected; $p < 0.025$, $\chi^2 = 5$, Yates correction). However, this difference may not reflect a nest site preference, but merely a difference in ease of discovery

between low and high exposure-visibility nestboxes. LINDAUER (1955) found that reducing the exposure of an unoccupied hive by piling brush over it enhanced its attractiveness as a nest site. MARTY (1949), BECKER (1967) and MARCHAND (1967) recommend when setting out bait hives to avoid both locations in full sun and places which are dark and obscure.

c) *Distance from parent nest.*

Measurements of the distances to new nest sites selected by swarms which were given full freedom in choosing a nest site are plotted in fig. 1. This

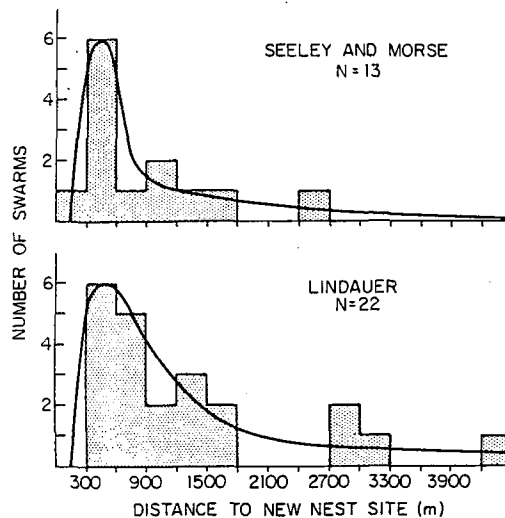


FIG. 1. — Distributions of distances to new nest sites, as calculated from the dances of scout bees. The curves are least-squares fits to points centered in the top of the histogram bars. Upper figure is original data; lower figure is after Table I in LINDAUER (1955).

ABB. 1. — Verteilung der Entfernungen zu den neuen Nistplätzen, aufgrund der Auswertung der Tänze der Spurbienen. Die Kurven sind nach dem Prinzip der kleinsten Quadrate durch Abgleichung der Punkte an der Spitze der Histogrammsäulen erstellt. Die obere Abbildung zeigt die neuen Daten, die untere Abbildung ist nach Tabelle I (LINDAUER, 1955) erstellt.

figure also includes data gathered in similar fashion by LINDAUER (1955) who observed swarms inside Munich and in various rural locations in West Germany. The striking features of the two distributions are (1) their similarity despite the widely separated study areas, and (2) the low frequency of swarms travelling less than 300 m to a new home site. The latter feature may simply reflect the smaller number of nest sites within a small relative to a large radius area. Or it could reflect the avoidance by swarms of nest sites within 300 meters of the parent nest. LINDAUER (1955) observed one swarm choose between

two identical hives, one 30 m and the other 250 m away, and select the distant hive. Beekeepers (MARTY, 1949; MARCHAND, 1967) report that placing bait hives 500 to 1,000 meters from an apiary is best, and that bait hives within 100 meters of apiaries are not likely to receive swarms.

Reduction of foraging competition with the parent colony probably favors wide swarm dispersal, whereas difficulties in long distance swarm flights would favor short movements. The curves in figure 1 may reflect the optimal compromise for honey bees of these opposing forces.

2. — Nest structure.

a) *Entrance area.*

The entrance areas of natural nests rarely exceed 60 cm² and are typically 10 to 20 cm² (SEELEY and MORSE, 1976). To test whether this pattern reflects the bee's preference in entrance size, we established 14 nestbox stations using nestboxes with two sizes of entrances. In each station one nestbox had a 4 cm diameter entrance hole while the other's entrance was 9.7 cm diameter, thus giving entrance areas of 12.5 cm² and 75 cm², respectively. The entrances were covered with 2.5 cm mesh « chicken wire » screening to discourage birds from inhabiting the nestboxes.

Six swarms occupied the small entrance nestboxes while none inhabited those with large entrances. This indicates a preference for the small entrance nestboxes ($p < 0.02$, one-tailed probability). A seventh small entrance nestbox was also occupied by a swarm, but because a small bird had built a nest in the large entrance nestbox at that station, this observation could not be counted. Statements in the beekeeping literature on the ideal entrance size for bait hives are conflicting. AVERY (1935) advocates a very small, about 4 cm² entrance hole, while MARTY (1949), CAILLAS (1946), BECKER (1967) and MARCHAND (1967) recommend « large » or « wide open » entrances. The latter authors used commercial beehives for which the maximum entrance area would rarely exceed 75 cm². Thus although large and not ideal, the entrances to their bait hives were apparently not so large that the hives were fully unsuitable nest sites.

Entrance size is probably a very important nest site property. The entrance is the focus of contact between the colony and the outside environment. This opening must be large enough for easy passage of foraging bees and air currents for nest ventilation, but cannot be so large that it would hamper colony defense or hinder control of the nest microclimate.

b) *Entrance shape.*

The significance of entrance shape was tested by providing a choice between nestboxes with circular or slit-shaped entrances of equal areas. These are the two typical entrance shapes in natural honey bee nests (SEELEY and

MORSE, 1976). The circular entrance was 3 cm in diameter; the slit entrance was 1×7 cm, with the large axis oriented vertically. Both types of entrance were positioned midway across the nestbox front, with the centers of the entrances 8 cm up from the floor of each nestbox.

Ten nestbox stations were established and 4 swarms occupied slit entrance nestboxes while 2 inhabited circular entrance nestboxes. A third swarm also occupied a circular entrance nestbox but interference by a colony of yellow-jacket wasps (*Vespula vidua*) in the slit entrance nestbox of the station made this observation meaningless for the test. This pattern of occupations indicates that there was no preference between entrance shapes under the conditions of the test ($p < 0.68$, two-tailed probability).

c) Entrance position.

Entrances in natural honey bee nests are disproportionately located in the bottom third of nest cavities (SEELEY and MORSE, 1976). To determine whether this pattern represents selection for bottom entrance nest cavities, we performed the following test. Twenty-four nestboxes with internal dimensions 20 cm wide \times 20 cm deep \times 100 cm tall were built. Twelve had their entrance (1.5 cm tall \times 6 cm wide) midway across the front side and at the very bottom of the nest cavity, flush with the nestbox floor. The other 12 nestboxes had their entrance at the very top of the nest cavity, flush with the nestbox roof. By using elongate nestboxes instead of cubes, we emphasized the difference between top and bottom entrances.

Twelve nestbox stations were established and 8 swarms inhabited the bottom entrance nestboxes and 2 occupied top entrance nestboxes. In addition, at one station both nestboxes were occupied within one inspection period and so yielded meaningless data. And at two stations in which the bottom entrance nestboxes were first occupied, the top entrance nestboxes were later also inhabited. These results show that bees preferentially occupied the bottom entrance nestboxes ($p < 0.06$, one-tailed probability) and that top entrance nestboxes, while less desirable, are nevertheless acceptable nest sites.

The advantages of a bottom entrance over a top entrance could include smaller convective heat loss (BÜDEL, 1960), simplified nest hygiene by facilitating removal of debris dropping to the nest bottom, or some other reason which might be related to the nest's organization of brood below and food above (SEELEY and MORSE, 1976).

d) Entrance direction.

The importance of entrance direction was analyzed using data generated during the tests of other nest site properties. First we noted the direction of the entrances in each nestbox station used in 1976 and 1977. Then each station was assigned to the directional group whose compass direction (N, NE, E, SE, S, SW, W, NW) was closest to the direction of the station's nestbox entrances.

Finally the 8 directional groups were compared with respect to their probabilities of having at least one nestbox occupation per station per year. We collected 124 nestbox station-years of data. Because this data was a by-product of other tests, the nestbox stations involved were composed of many different kinds of nestboxes. However, as is shown in table I, no one type of nestbox station received swarms with a probability significantly different from the others. Thus there was no possibility that a particularly high or low attractiveness to one or two nestbox types could have been coupled with a non-uniform distribution in the entrance directions of these nestboxes to bias the directional probabilities of nestbox occupation.

TABLE I. — Occupation probabilities for different types of nestbox stations.

TABELLE I. — Wahrscheinlichkeiten für das Beziehen verschiedener Arten künstlicher Nistplätze.

Station type	Number of stations	Probability of at least one occupation station/year	Probability of no significant difference from \bar{p}
Nest height	8	0.75	> 0.51
Entrance area	14	0.50	> 0.54
Entrance shape	10	0.70	> 0.68
Entrance position	12	0.92	> 0.16
Volume preference (a)	14	0.78	> 0.43
Volume resolution (a)	20	0.35	> 0.19
Cavity shape	12	0.75	> 0.51
Cavity dryness	10	0.50	> 0.54
Cavity draftiness	12	0.58	> 0.84
Comb in cavity.....	12	0.33	> 0.17
	<u>124</u>	<u>$\bar{p} = 0.62$</u>	

(a) The experiments involving this type of nestbox station were described in SEELEY (1977).

Figure 2 compares the probabilities of at least one occupation/station/year for the eight compass directions. Nestbox stations whose entrances faced SE, S and SW showed a significantly higher average annual probability of at least one occupation ($\bar{p} = 0.84$) relative to stations with entrances facing W, NW, N, NE and E ($\bar{p} = 0.51$), ($p < 0.05$, two-tailed probability).

This preference of southward over northward entrances may reflect a difference in entrance insolation. Beekeepers in the northern hemisphere regularly face their colonies to the south because they believe bees forage more actively and overwinter better in hives with sunlit rather than shaded entrances.

e) *Cavity volume.*

Studies of the honey bee's preference in nest cavity volume are reported elsewhere (SEELEY, 1977). The present treatment of this topic is a brief review of previous findings.

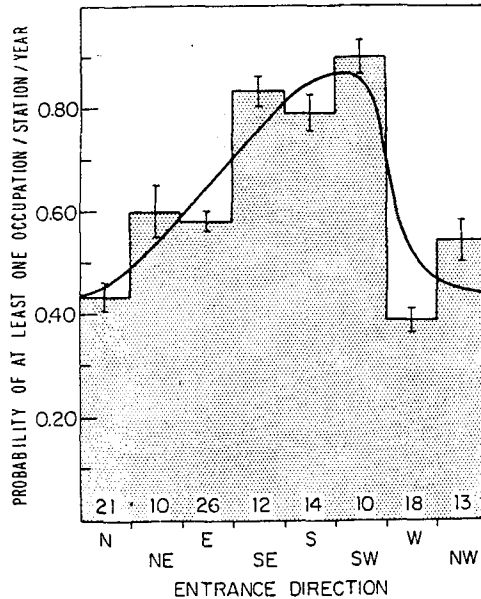


FIG. 2. — Probability of nestbox occupation as a function of entrance direction. Vertical bars denote plus or minus one standard error. The curve is a least-squares fit through points centered in the top of each histogram bar. Numbers along the abscissa denote the number of nestbox station-years for each of the eight directions; total : 124 station-years.

ABB. 2. — Wahl eines Nistplatzes als Funktion der Richtung des Eingangs. Die vertikalen Linien an der Spitze der Histogrammsäulen bezeichnen die Standardfehler. Die Kurve ist nach dem Prinzip der kleinsten Quadrate durch Abgleichung der Punkte an der Spitze der Histogrammsäulen erstellt. Die Zahlen auf der Abszisse bezeichnen die Anzahl der Nistplatz-Jahre für jede der acht Richtungen; Gesamtzahl : 124 Nistplatz-Jahre.

LINDAUER (1955) produced the first evidence for volume selection during nest site selection in observing that a very small swarm rejected his nestboxes until he halved the volume of one, whereupon the swarm promptly inhabited the reduced volume nestbox. SEELEY and MORSE (1976) found that the volume distribution of natural nests has a wide range (12 to 443 liters observed), but that most nest volumes are clustered in the 20 to 100 liter subrange. SEELEY (1977) demonstrated that this distribution reflects volume selection among potential nest cavities. Swarms prefer 40 liter over 10 and 100 liter nest cavities. The function of this volume selection may be twofold : 1) avoidance of cavities too small to enclose an entire colony, and 2) control of mature colony size by limiting the space available for colony growth.

Given the existence of volume selection in nest cavities, there appears to be considerable geographical variation in the preferred cavity size. From

descriptions of the sizes of natural nests (SCHMIDT, 1897; WADEY, 1948; LINDAUER, 1955; SEELEY and MORSE, 1976) and direct experiments (SEELEY, 1977) one can conclude European honey bees prefer nest cavities in the range of 20 to 80 liters. However, in the Bashkir region of the Soviet Union, honey bees rarely occupy tree cavities smaller than 40 liters, suggesting that the lower limit of acceptable cavity size is about 40 liters for these bees (PETROV, 1970). At the other extreme, the originally African honey bees now in South America readily occupy 10 liter or even smaller nestboxes (O. R. TAYLOR, personal communication). In Africa a wide range of effective bait hive sizes has been reported. The upper limit is about 300 liters while the typical hive size is about 100 liters (SMITH, 1960; BROKENSHA *et al.*, 1972; REA, 1974).

f) *Cavity shape.*

Most natural nests have approximately the form of an elongate, upright cylinder (SEELEY and MORSE, 1976). Although this generalization probably reflects the pattern of wood decay in standing trees, we tested whether bees prefer tall, elongate cavities over cube-shaped cavities. Twelve nestbox stations were established, each containing one tall nestbox (20 × 20 × 100 cm) and one cubical nestbox (34.2 × 34.2 × 34.2 cm). For both nestbox types the entrance consisted of an opening 1.5 cm tall × 6 cm wide located at the base of the nestbox, midway across the front side.

At 6 stations the cube nestbox was occupied and at 3 stations the tall nestbox was inhabited, thereby demonstrating no significant shape preference under the test conditions ($p < 0.01$, one-tailed probability). At one station in which the tall nestbox was first inhabited, the cube nestbox was later also inhabited.

g) *Cavity dryness.*

Honey bee colonies can keep their nests dry by selecting dry nest cavities or by waterproofing wet ones. The propolis coating of the cavity walls in natural nests (SEELEY and MORSE, 1976) suggests that bees can waterproof their nests. To determine whether bees select dry nest sites, we performed the following test. First we added 2 liters of a mixture of dried sawdust and dried punkwood to every nestbox used in this test. To ensure uniform material for the two nestboxes in each station, we prepared 4 liter batches of the sawdust-punkwood mixture with thorough mixing and then divided each one between the two nestboxes of each nestbox station. For one nestbox in each station, the « wet nestbox », the sawdust-punkwood mixture was heavily wetted by mixing it with 1 liter of water before placing it inside the nestbox. The « dry nestbox » was prepared by leaving the sawdust-punkwood mixture dry when placing it inside its nestbox. Ten nestbox stations were established. Whenever these stations were inspected, the sawdust-punkwood layer of each wet nestbox was again wetted with a liter of water. Interior inspections of these nestboxes

showed that wet nestboxes were continuously wet inside while the dry nestboxes stayed dry.

At 2 stations the dry nestbox was inhabited while at 3 stations the wet nestbox was occupied, thus indicating no preference of the dry over the wet nestboxes ($p < 0.81$, one-tailed probability). In nature, many nest cavities are lined with wet, decaying wood when bees first inhabit them (SEELEY and MORSE, 1976). Bees quickly scrape clean the inner surfaces of such cavities and coat them with water-proofing propolis. Perhaps because cavity wetness is a nest site property which bees can remedy, bees do not weight this factor heavily when evaluating potential nest sites.

h) *Cavity draftiness.*

To test the importance of nest cavity draftiness, we established 12 nestbox stations in which one nestbox had its front and sides each perforated by 25 holes (6.35 mm diameter) spaced 6 cm apart in a grid pattern (drafty nestbox) and the other nestbox was identical but lacked such holes (sound nestbox).

At 3 stations the sound nestbox was occupied and at 4 stations the drafty nestbox was inhabited. These results indicate no preference of sound over drafty nestboxes ($p < 0.77$, one-tailed probability). The reason for this counter intuitive outcome may resemble that for the bee's equal acceptance of wet and dry nestboxes. Like cavity wetness, cavity draftiness is a nest site variable which bees can modify by filling in cracks and holes with propolis. Therefore they are not forced to deal with a cavity's draftiness just at the time of choosing their nest site. For example, the swarms which occupied drafty nestboxes quickly plugged with propolis the numerous holes in their nest cavities' walls.

i) *Comb Inside the Cavity.*

The first year is the most hazardous year in the life of a honey bee colony. Only about one quarter of all feral colonies in the Ithaca area survive the founding year (SEELEY, 1978). The reason for this high mortality is that in the first year a new colony must accomplish the multiple tasks of finding and occupying a nest site, building a nest, rearing brood and stockpiling winter food, all in the remaining summer season. It therefore seems highly profitable to eliminate one of the many hurdles involved in colony founding by inhabiting a pre-existing nest. Wild honey bee swarms have been recorded inhabiting already constructed nests which were vacated by the deaths of their colonies (SEELEY, 1978).

Our test of the effect of comb inside a nest cavity involved 12 nestbox stations in which one nestbox contained an approximately 15×20 cm portion of dark, old comb and the other nestbox contained no comb. Only 4 nestbox stations received swarms. In 3 stations the comb-containing nestbox was occupied. In the fourth station the combless nextbox received the swarm.

However, inspection of the nestbox containing comb in this fourth station revealed a colony of yellowjacket wasps (*Vespula arenaria*) and approximately 20 earwigs (Dermaptera). With only 3 clear selections of the comb-containing over the combless nestbox, the bee's preference for cavities with comb is neither disproven nor significantly ($p < 0.13$, one-tailed probability) substantiated.

The universal recommendation by beekeepers to include old combs inside bait hives (CAILLAS, 1946; MARTY, 1949; BECKER, 1967; MARCHAND, 1967; GUY, 1971) and the standard practice in Africa of smearing bait hive interiors with beeswax (SMITH, 1960; ROBERTS, 1971; BROKENSHA *et al.*, 1972) both suggest that combs of a previous colony enhance a nest site's attractiveness. And in the bee forests of medieval Russia, tree cavities once occupied by bees were valued more highly than cavities which had not been occupied (GALTON, 1971). This value difference probably reflected a difference in attractiveness to swarms between previously and never inhabited sites.

DISCUSSION

The principal significance of the present study is its detailed confirmation of LINDAUER'S (1955) finding that for the honey bee, nest site selection is a complex process in which many properties of a potential nest site's location and structure are evaluated. Moreover, the preferences in nest site variables appear appropriate for the honey bee's behavior and ecology. The preference for an elevated, previously occupied nest site which is beyond 300 m from the parent nest and which has a small, southward facing entrance near the nest bottom, can be reasonably interpreted in terms of adaptations for improved colony defense and foraging, simplified control of the nest microclimate, and economy in nest construction. Also, the variables of cavity dryness and draftiness, although important to finished nests, are not weighted heavily during nest site selection, apparently in reflection of the bee's ability to modify these properties of a nest site. The relationships between the honey bee's ecology and its preferences in nest site properties are summarized in table II.

Further studies of nest site selection by honey bees could follow several avenues of investigation. Using factorial design experiments, one could analyze how bees weight the different nest site variables in computing the overall quality of a nest site. Also, it would be interesting to learn more about the sensory mechanisms underlying a scout bee's perceptions of the important nest site properties (see, for example, SEELEY, 1977). However, the most important next step in studying nest site selection is to test the adaptive significance of the observed nest site preferences by comparing the fitnesses of colonies in hives whose designs and locations reflect or contradict the bees preferences in nest site properties.

TABLE II. — Relationships between preferences in nest site properties and honey bee ecology.

TABELLE II. — Beziehung zwischen Bevorzugen von Nistplatzeigenschaften und der Ökologie der Honigbiene.

Nest site property	Preference (a)	Probable underlying ecological factor(s)
1. Nest height.	5 > 1 m	Colony defense.
2. Nest exposure-visibility.	High > low (b)	Ease of nest site discovery.
3. Distance from parent nest.	Beyond 300 m	Foraging competition with parent nest.
4. Entrance area.	12.5 > 75 cm ²	Colony defense, nest microclimate control.
5. Entrance position.	Bottom > top	Nest hygiene and microclimate control.
6. Entrance direction.	Southward > northward	Insolation for foraging and nest microclimate control.
7. Cavity volume.	10 < 40 > 100 liters	Minimum and maximum colony size.
8. Cavity dryness.	None (c)	Bees waterproof nests.
9. Cavity draftiness.	None (c)	Bees seal nests.
10. Comb in cavity.	With > without (d)	Economy in nest construction.

(a) « A > B » means « A preferred over B ».

(b) Sheltered, low visibility sites may be preferred once they are found.

(c) No preference under the *particular conditions* of our experiment.

(d) Statistical significance, $p < 0.13$.

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