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THE NEST OF THE HONEY BEE (*APIS MELLIFERA* L.)

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SUMMARY

The natural honey bee nest was studied in detail to better understand the honey bee's natural living conditions. To describe the nest site we made external observations on 39 nests in hollow trees. We collected and dissected 21 of these tree nests to describe the nest architecture. No one tree genus strongly predominates among bee trees. Nest cavities are vertically elongate and approximately cylindrical. Most are 30 to 60 liters in volume and at the base of trees. Nest entrances tend to be small, 10 to 40 cm^2, and at the nest bottom. Rough bark outside the entrance is often smoothed by the bees. Inside the nest, a thin layer of hardened plant resins (propolis) coats the cavity walls. Combs are fastened to the walls along their tops and sides, but bees leave small passageways along the comb edges. The basic nest organization is honey storage above, brood nest below, and pollen storage in between. Associated with this arrangement are differences in comb structure. Compared to combs used for honey storage, combs of the brood nest are generally darker and more uniform in width and in cell form. Drone comb is located on the brood nest's periphery. Comparisons among *Apis* nests indicate the advanced characters in *Apis mellifera* nests arose in response to *Apis mellifera's* adoption of tree cavities for nest sites.

RÉSUMÉ

Le nid de l'Abeille domestique (*Apis mellifera* L.).

Nous avons étudié en détail le nid naturel de l'Abeille pour mieux comprendre l'écologie de cette espèce. Afin de décrire le site du nid, nous avons fait l'inspection extérieure de 39 nids dans les arbres creux. Pour en étudier la structure, nous avons récolté et disséqué 21 d'entre eux. Les arbres où sont trouvés les nids appartiennent à des genres divers. Les cavités qui abritent les nids sont à peu près cylindriques; elles sont étroites et allongées selon la verticale. La plupart des cavités ont un volume de 30 à 60 litres et se localisent au pied des arbres. Située à la base du nid, l'entrée est de 10 à 40 cm². A l'extérieur de l'entrée, l'écorce auparavant rugueuse est souvent aplanie par les Abeilles. A l'intérieur du nid, une couche mince de résine végétale durcie (propolis) recouvre les parois de la cavité. Les rayons sont rattachés aux parois par le haut et les côtés, mais les Abeilles laissent de petits passages le long des rayons. L'organisation fondamentale du nid comporte le stockage du miel dans les alvéoles supérieurs, l'élevage du couvain dans les alvéoles inférieurs et le stockage du pollen dans les alvéoles intermédiaires. A cette répartition sont associées des différences de structure dans les alvéoles. Par rapport à ceux qui contiennent du miel, les alvéoles à couvain sont généralement de couleur plus foncée et sont plus uniformes dans leur profondeur et leur forme. Les alvéoles de mâles sont localisés à la périphérie du nid à couvain. La comparaison entre nids du genre *Apis* indique que certains caractères avancés du nid d'*Apis mellifera* ont évolué en réponse à l'adoption par cette espèce de cavités d'arbres comme sites de nidification.

INTRODUCTION

The honey bee's *(Apis mellifera)* natural nest has remained almost wholly unexplored to the present time. Previously only superficial observations on nests in trees (GOSSE, 1844; SCHMIDT, 1897; PHILLIPS, 1917; WADEY, 1948; HOYT, 1965), detailed descriptions of the atypical open air nest (BOUVIER, 1904, 1905, 1906) and an experimental analysis of the nest site (LINDAUER, 1955) were available in the literature. The attraction for studying the natural nest is heightened by the need to know the honey bee's natural living conditions to fully understand the functions of this insect's social behavior. In this paper we describe the nests of honey bee colonies inhabiting hollow trees and so describe part of the honey bee's natural ecology.

METHODS AND MATERIALS

Study area. We collected nests in the vicinity of Ithaca, N. Y. Numerous feral honey bee colonies inhabit the unmanaged, mature forests of this agricultural region. Ithaca has a humid, continental type climate with warm summers and long, cold winters (DETHIER and PACK, 1963).

Honey bee races. The honey bees whose nests we studied were a hybrid of the many 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 U.S. and California into the Ithaca area by the approximately 100 hobby and 3 commercial beekeepers of this region. Therefore, the bees whose nests we examined were probably a cross section of North American honey bees.

Type of nests. We studied in detail only nests in hollow trees. Figure 1 shows one such nest exposed. Because we considered nests in man-made structures as unnatural and open air nests as atypical, we did not examine these nests in detail (1).

(1) We encountered nests in many man-made and two other natural nest sites besides tree cavities. Man-made sites included walls of buildings, chimneys, birdhouses, a barrel, an ironstove, an overturned armchair, and wooden boxes. The two other natural sites were a cave and open tree branches. Measurements of these nests are not included in this paper.

FIG. 1. — Exposed honey bee nest in tree cavity showing several nest characteristics : vertically elongate shape ; small entrance (knothole through left wall, indicated by arrow) ; nest organization of honey above, brood below; and drone comb at edge of brood nest. Two outer combs were removed to expose the brood nest. Entire nest is 150 cm tall.

FIG. 1. — Aspect d'un nid naturel d'*Apis mellifera* dans la cavité d'un arbre. Le nid s'allonge selon la verticale; l'entrée est indiquée par la flèche; le miel est stocké dans les alvéoles supérieurs, le couvain occupe les alvéoles inférieurs; les alvéoles de mâles se trouvent en bordure du nid à couvain. Les deux rayons les plus externes ont été enlevés pour montrer le nid à couvain. Le nid s'étend sur 1,50 m en hauteur.

Finding nests. We found 39 nests by random searching, lining bees (EDGELL, 1949), advertising in newspapers and asking resident beekeepers.

Determining nest age. The owner of each bee tree frequently had observed the bees in his bee tree for one or more years. This gave us minimum ages for these nests. We recognized nests less than one year old by their small comb area and their white to very light yellow combs.

Nest collection. We collected 21 nests for dissection. Before collecting a nest, details of the nest site were recorded with descriptions and photographs. We measured the exposure of nest sites to wind, sun and rain by rating the tree section enclosing the nest on a three-point exposure scale : 1 (low), 2 (medium), 3 (high). Collecting a nest involved sawing down a tree and cutting free the tree portion enclosing the nest. Two measures were taken to ensure the collection of complete nests. First, the night before collecting a nest we killed the colony and sealed the entrance. Second, whenever possible, we did not open nests before dissecting them in the laboratory.

Nest dissection. Each nest was opened by splitting off one side of the log enclosing the nest. Dissection data were recorded in descriptions, sketches and photographs. We measured comb areas with a grid of 2.5 cm sided squares and measured the honey in nests by weighing combs containing honey. To count colony populations, we picked the dead bees from the nest, directly counted the conspicuously larger drones and estimated the worker population by weighing the mass of dead workers and a sub-sample of 2,000 workers. Cavity diameter was recorded as the average of diameter measurements made at 20 cm intervals along the nest cavity. We determined the volume of nest cavities by volumetrically filling the tree hollow with sand after removing the combs.

RESULTS AND DISCUSSION

1. Nest site.

Tree type. Table I is the distribution of tree types for 30 bee trees. We observed 12 tree genera and the most common genus, *Quercus,* predominated only slightly. Angiosperms strongly outnumbered gymnosperms. The distribution probably reflects the abundance and susceptibility to decay of the 12 tree genera. However, honey bees may prefer certain tree types for nest sites. If so, our data indicate that either their preference is weak or it is severely constrained by the availability of hollows in trees.

Tree condition. Only 75 % (N = 36) of the bee trees were alive. However, all were very solid and provided sturdy nest walls. Thus bees inhabit trees which are hollow and sturdy but not necessarily alive.

Exposure. We obtained the following mean exposure values from measurements on 36 nests : wind, $\bar{x}$ = 2.02 (SD = 0.77); sun, $\bar{x}$ = 1.82 (SD = 0.80); rain $\bar{x}$ = 1.84 (SD = 0.82). Values of 1 and 3 denote low and high exposures,

TABLE I. — Frequency distribution of tree genera for 30 bee trees.

TABLEAU I. — Distribution des fréquences du genre des arbres abritant 30 ruches sauvages.

Tree	Percentage of bee trees
Oak *(Quercus)*	20.0
Walnut *(Juglans)*	13.4
Elm *(Ulmus)*	10.0
Pine *(Pinus)*	10.0
Hickory *(Carya)*	10.0
Ash *(Fraxinus)*	10.0
Maple *(Acer)*	6.7
Basswood *(Tilia)*	6.7
Beech *(Fugus)*	3.3
Apple *(Pyrus)*	3.3
Hemlock *(Tsuga)*	3.3
Cedar *(Juniperus)*	3.3

respectively. The typical nest site is therefore moderately exposed to wind, partially shaded and moderately wetted by rain. Both heavily exposed trees in clearings and trees thickly sheltered by brush represent uncommon nest sites. However, our exposure data may have been biased by a systematic sampling error. Because nests had to be first noticed by someone to be included in this study, we may have examined nests which were more exposed than average.

Shape and size. All nest cavities were vertically elongate and approximately cylindrical. Measurements of 17 nests provided the following data. Maximum and minimum cavity diameters were 42.7 cm and 15.2 cm. Maximum and minimum cavity heights were 351 cm and 49 cm. The mean cavity diameter, height and (height/diameter) ratio were 22.7 cm (SD 6.6 cm), 156 cm (SD 83 cm) and 7.2 (SD 3.8), respectively. Except for new nests and one nest in a 448 liter tree hollow, all nests filled their nest cavities. Typically then, a nest cavity and the nest inside the cavity possess the same shape and size.

FIG. 2. — Distribution of nest volumes for 21 nests.

FIG. 2. — Distribution des volumes occupés par 21 nids.

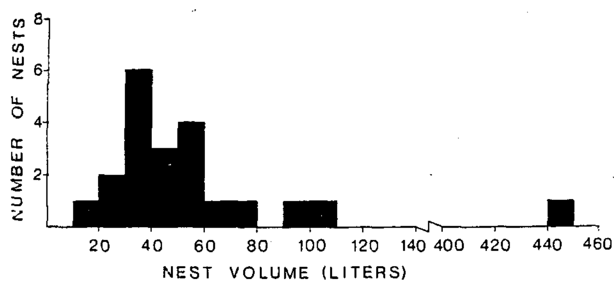

Figure 2 shows the distribution of nest volumes. The distribution approximates a normal distribution about the median volume of 45 liters. Prior observations support this distribution. SCHMIDT (1897) observed an approximately 34 l nest cavity. WADEY (1948), after examining over 50 feral colonies, suggested a 44 to 57 l hive design. One of LINDAUER's (1955) normal sized swarms chose a 30 l underground cavity for a home. And MARCHAND (1967) successfully trapped swarms in 17 to 42 l nest boxes. PERCIVAL's (1954) approximately 630 l nest holding 200 kg of honey was probably exceptionally large.

The distribution of nest volumes may reflect the distribution of available cavity sizes, a preference in nest volume by bees, or an interaction of the two. LINDAUER (1955) found that honey bees note cavity size when evaluating potential home sites.

2. Nest architecture.

Construction materials. We observed only beeswax and propolis as building materials in nests. Honey bee salivary secretions, kneaded into the wax during comb construction, are a third but invisible building material. Bees sometimes substitute wet paint and petroleum products for propolis (RIBBANDS, 1953), but we did not observe these substances in nests.

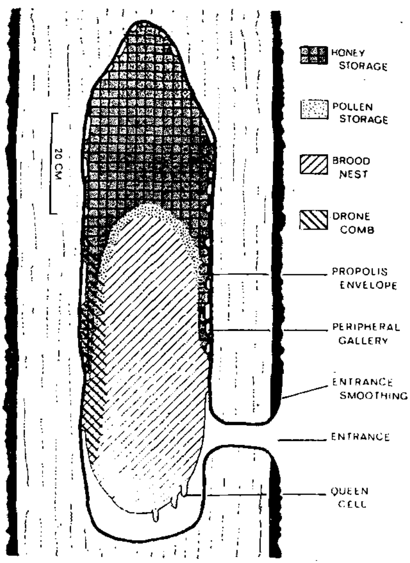

FIG. 3. — Diagram of honey bee nest.

FIG. 3. — Diagramme d'un nid.

Nest organization. Figure 3 represents a longitudinal cross section through a generalized honey bee nest. The major nest structures are labelled. The nest occupies an elongate tree cavity accessed through a small entrance hole. Honey and pollen are stored above and alongside the brood nest. Drone comb is on the edge of the brood nest. Propolis coats the cavity walls. The tree bark is smoothed around the nest entrance.

Entrance. We inspected 49 entrances in 33 nests. Knotholes (56 %), tree cracks (32 %) and holes among roots (12 %) formed entrances. Most nests (79 %) had one entrance. The others (21 %) had up to 5 entrance holes. The mean distance between an entrance's outer opening and the nest cavity was 15.3 cm (SD 7.5 cm, N = 18); the maximum distance was 74 cm.

GOSSE (1844) noticed that bees had smoothed the bark about the entrance of a honey bee nest. We confirmed his report in observing areas of smoothed bark extending up to 30 cm from entrance holes. Figure 4 shows an example of this entrance smoothing. The entrance areas of older nests were generally more polished than those of younger nests. « Washboard » behavior, in which young bees thrust their bodies back and forth while scraping a surface with their mandibles and foreleg tarsi (GARY, 1975), is probably part of the entrance smoothing operation. Apparently rough bark is scraped down and the remaining cracks are filled with propolis to create the smoothed area. The area is not sticky. We can only speculate upon the functions of this entrance smoothing. Perhaps it improves surveillance for nest defense and facilitates traffic flow at the nest entrance.

Figure 5 shows the distribution of entrance sizes for 33 nests. Entrances were small relative to the nest cavity. Most nests (70 %) had entrances smaller than 40 cm². The modal entrance area was 10 to 20 cm². We did not observe any entrances reduced in area with propolis, as characterizes *Apis mellifera caucasica* nests (RUTTNER, 1968 *b*). Entrance size is probably an important detail in nest design. The entrance is the interface between nest and environment. Through it must pass all the bees, air, food and construction materials of the colony. If bees exert a preference in entrance size during home site selection, it probably involves a compromise. A large entrance, good for summer ventilation and labor flow, is poor in the winter and at times of nest defense.

FIG. 4. — Smoothing around nest entrance (indicated by arrow). Bees have gnawed the rough bark and filled cracks with propolis.

FIG. 4. — Exemple d'aplanissement de l'écorce autour de l'entrée du nid (flèche blanche). Les Abeilles ont « mâché » l'écorce rugueuse et rempli les fentes de l'écorce avec de la propolis.

Figure 6 shows that most entrances were at or near ground level. This distribution also represents the distribution of nest heights since nest cavities were generally immediately adjacent to nest entrances. The predominance of ground level nests probably reflects a predominance of tree cavities at the bases of trees. Alternatively, bees may select ground level cavities for their presumed greater shelter and sturdiness relative to cavities higher in trees.

The space in front of the nest entrance generally was clear and provided an open flight path. To an eye positioned 2 m straight out from an entrance, 93 % of the entrances were plainly visible but 7 % were not visible (41 entrances from 31 nests). Intervening grass, brush or branches obscured entrances in this latter group.

Nest entrances tended to be near the nest bottom. By classifying nest entrances as opening into the bottom, middle or top third of the nest cavity, we obtained the following distribution : bottom, 58 %; middle, 18 %; top, 24 % (29 entrances from 20 nests). This predominance of bottom entrances is highly improbable ($P < 0.002$) assuming entrance position relative to the cavity is random. This nonrandom distribution can be explained in two ways. Either

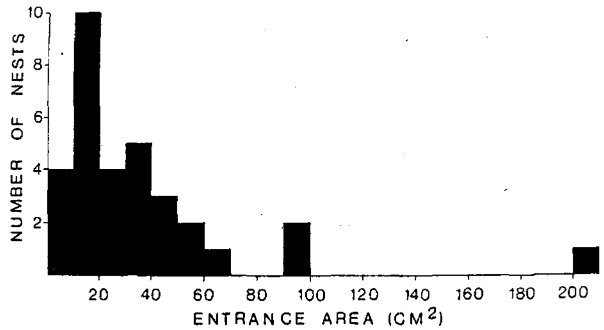

FIG. 5. — Distribution of entrance size for 33 nests.

FIG. 5. — Distribution des surfaces du trou d'entrée dans 33 nids.

FIG. 6. — Distribution of entrance heights for 49 entrances.

FIG. 6. — Distribution des hauteurs de 49 trous d'entrée.

honey bees select cavities with bottom entrances, or fungal decay, which probably produces most tree cavities, tends to expand upward from its entry point into a tree. A bottom entrance is probably advantageous. Convectional heat loss is smaller for nests with the entrance at the bottom than at the top (BÜDEL, 1960).

The distribution of entrance directions relative to the earth was random (entrance direction-number of entrances) : N - 2, NE - 4, E - 4, SE - 4, S - 6, SW - 8, W - 7, NW - 6 (41 entrances from 31 nests).

Walls. The walls of nest cavities were always solid (see 1. Nest Site, *Tree condition*) and coated with propolis on their inner surfaces. Figure 7 shows a small area of this propolis coating. In finished nests the propolis layer was thick and completely covered a nest cavity's floor, walls and ceiling to form the propolis envelope drawn in figure 3. The thickness of this layer varied between 0.1 and 2.3 mm, but was generally in the 0.3 to 0.5 mm range.

We dissected several unfinished nests and thus observed the intermediate stages in the preparation of nest cavity walls. When combs only partially filled a cavity, the nest cavity's inner surface was solid and smooth with propolis only around the combs. Lower in the cavity, below the level of the combs, a layer of soft, rotten wood coated the cavity walls. This punkwood lining was up to 20 mm thick. Apparently, before bees build combs they scrape the loose, rotten wood off the walls, thereby exposing firm wood which they then coat with propolis.

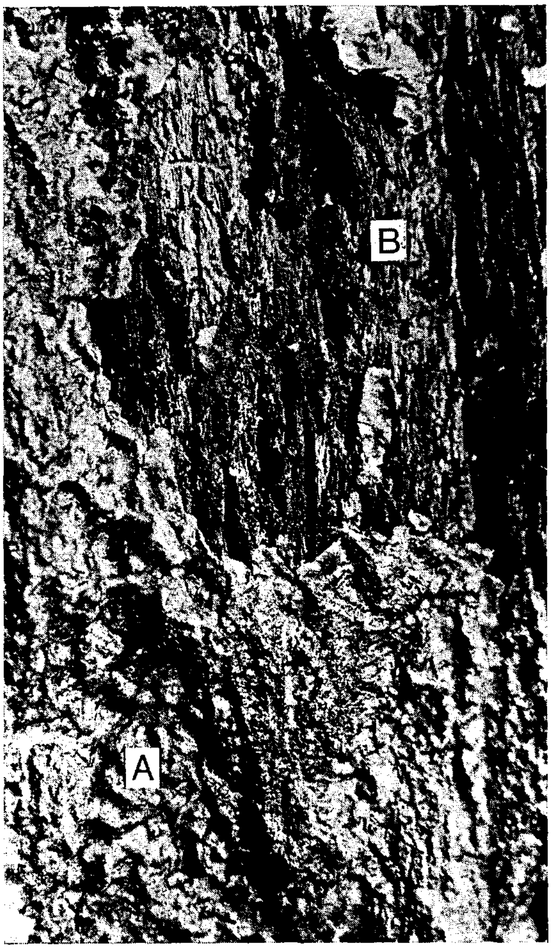

FIG. 7. — Propolis coating of nest wall (region A). Propolis was chipped off in the upper right (region B). The wall area shown is 8 cm by 12 cm.

FIG. 7. — Revêtement de propolis sur les parois extérieures du nid (région A). La propolis a été écaillée dans la région B. La surface représentée a des dimensions de 12 cm × 8 cm.

This preparation of cavity walls probably serves many functions. First, clean and solid walls are essential for tight comb attachment. Also, nest defense and homeostasis of the nest atmosphere are certainly simplified by the propolis envelope which plugs small openings. Nest sanitation is probably improved since propolis is bacteriocidal (LAVIE, 1968). And since propolis repels water, the propolis envelope may waterproof the nest from tree sap and other external moisture. Furthermore, because polypore fungi probably produce the nest cavities (GRAY, 1959), honey bees may face the problem of continued fungal decay of their nest cavity walls. The two actions of scraping decaying wood off the cavity walls, which removes fungal mycelia, plus coating the cavity walls with propolis, which is waterproof and fungicidal (LAVIE, 1968), may inhibit the wood rotting fungi. Finally, WALRECHT (1962) ascribes a communication function to

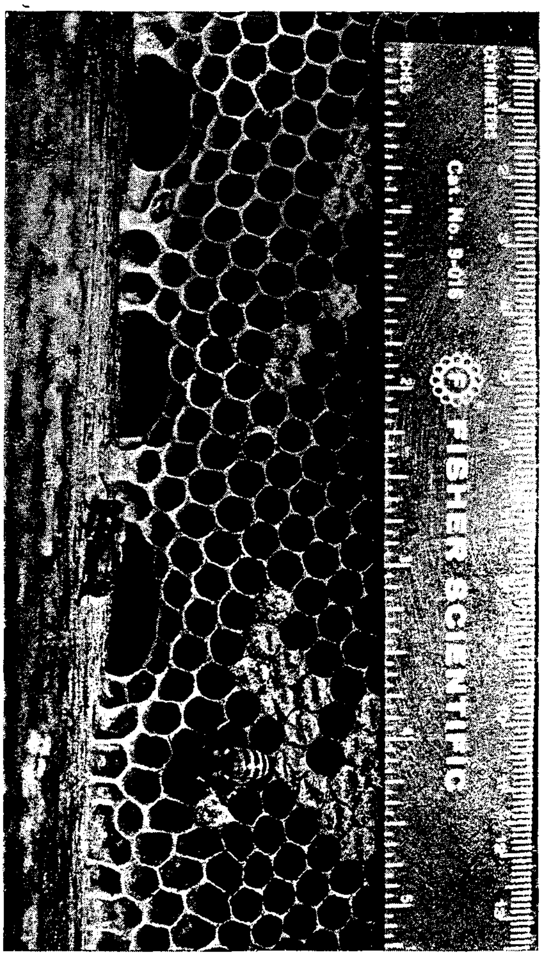

FIG. 8. — Three peripheral galleries.

FIG. 8. — Trois passages aménagés par les Abeilles en bordure d'un rayon.

the propolis layer : propolized walls signal completion of that portion of the nest.

Combs. Von FRISCH (1974) and WERNER-MEYER (1960) describe in detail the structure of honey bee combs. HUBER (1814), DARWIN (1859), WERNER-MEYER (1960), MARTIN and LINDAUER (1966), and DARCHEN (1968) describe comb construction. THOMPSON (1942) reviews the mathematical study of the form of honey bee cells. We now describe the orientation, suspension, utilization pattern and different forms of combs in natural honey bee nests.

Nests contained up to eight combs. Combs were generally planar and in parallel alignment, but deviations from planarity were observed. In cavities 20 cm or less in diameter, combs spanned the cavities in neat planes. But in cavities with larger diameters, combs were sometimes curved. Small combs filled the spaces between curved combs. We noted in 15 nests the direction of the main plane in which combs were aligned. The directions of these planes were randomly distributed with respect to both the nest entrance and the earth. ULRICH (quoted by WERNER-MEYER, 1960) had previously demonstrated random comb orientation with respect to the entrance.

Each comb was attached to the cavity walls along its top and sides, but hung free along its bottom edge. Between cavity floor and comb bottom there remained several centimeters of open space. The attachment along the top and sides was intermittent. As shown in figures 3 and 8, bees build small passageways along the comb edge. Without these holes, the combs would span the nest cavity like solid curtains and prevent free circulation of bees about the nest. We termed these passageways « peripheral galleries ».

The general organization of the nest seemed to reflect the pattern of comb attachment to the cavity walls. In these approximately cylindrical nests, honey was stored in the upper and peripheral nest regions. The brood nest was below the honey and toward the center of the nest. Pollen was between brood and honey (fig. 3). This arrangement, which places the heavier honey near points of comb attachment and the lighter pollen and brood away from attachment points, may serve to minimize internal stress within the wax combs. The open space beneath combs permits elongate queen cells to project downward off the bottoms of combs.

Several differences in comb structure were often associated with the functional separation of nests into honey bearing regions and brood and pollen bearing regions. Table II provides a systematic comparison of these differences. Figure 9 shows the differences in uniformity of comb width, cell wall curvature, cell size variation and color between combs of the honey storage and brood nest regions. Comparison of upper and lower comb areas in the figure 1 nest reveals the difference between the two nest regions in regularity of cell pattern.

TABLE II. — Comparison of brood comb [a] and honey comb [b].

TABLEAU II. — Comparaison entre les rayons du nid à couvain et les rayons à miel.

Brood comb	Honey comb
Comb width is uniform : worker comb [c], 21-24 mm wide, drone comb [d], 25-29 mm wide.	Comb width is variable.
Cell walls are straight.	Cell walls are often curved.
Cell size is uniform : cells are either worker cells or drone cells.	Cell size is variable : cells are of various diameters and depths.
Cell cross section : regularly hexagonal.	Cell cross section : often irregularly hexagonal.
Cell pattern is regular : cells arranged in straight, horizontal rows.	Cell pattern is often irregular : cells often arranged in curved series.
Color is dark brown or black.	Color is often light yellow to light brown.

[a] Comb bearing brood and pollen, in the lower and central regions of the nest.
[b] Comb bearing honey, in the upper and peripheral regions of the nest.
[c] Comb composed of worker cells.
[d] Comb composed of drone cells.

Since newly built combs have regular cell shapes and patterns, we interpret the structural irregularities in the honey storage combs (except for the comb width variation) as distortions induced after comb construction by the heavy honey they hold. Such distortion is familiar to beekeepers when they do not

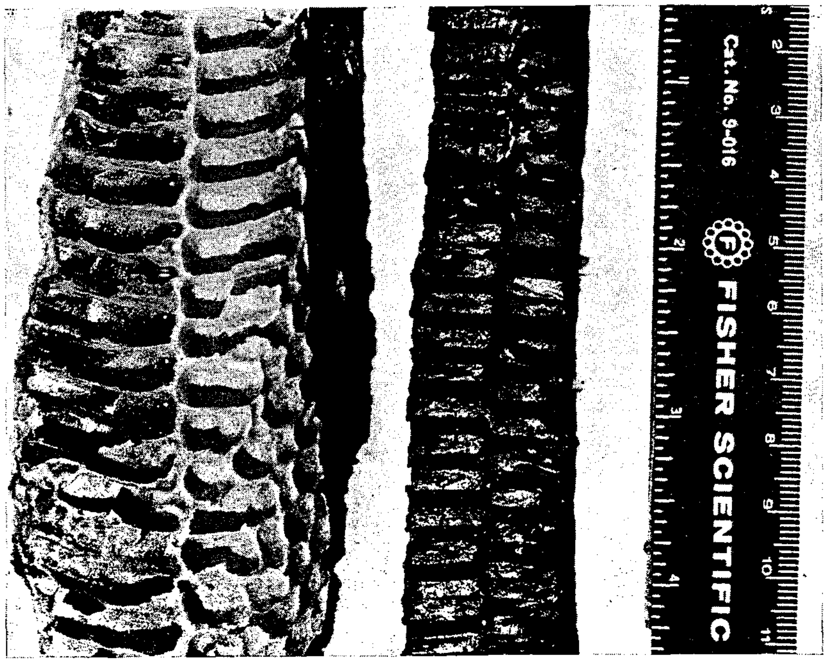

Fig. 9. — Comparison of brood nest comb (right) and honey storage comb (left).

Fig. 9. — Comparaison entre les alvéoles du nid à couvain à droite et les alvéoles à miel à gauche.

reinforce their honey combs with wires embedded in each comb's midrib. Combs of the brood nest, bearing the lighter load of brood and pollen, could maintain their regular cell shapes and pattern. Irregular cells are satisfactory honey containers, but uniformity in size and shape may be essential for cells used in brood rearing.

We found drone comb on the edges of brood nests, sometimes as a peripheral band on an inner comb (fig. 3), other times as an entire outer comb. Other investigators (Free, 1967; Taber and Owens, 1970; Owens and Taber, 1973) report the same location of drone comb. The grouping of drone cells into drone comb probably simplifies the honey bee's sex determination system. This arrangement frees queens from constantly switching between laying fertilized and unfertilized eggs.

Table III shows the amount of drone comb in eight nests. We counted as drone cells only the brood nest cells with drone cell dimensions. Thus we excluded from our count the large cells resembling drone cells in the upper, honey storage region of the nest. This table shows relative uniformity in the proportion of drone comb among eight nests. Whereas the absolute amount of drone comb varied widely (SD 1,240 cm^2) about the mean area of 3,880 cm^2, the percentage of the total comb area devoted to drone comb varied relatively

TABLE III. — Amount of drone comb in eight nests [a]. Each nest's cavity was filled with combs.

TABLEAU III. — Nombre de cellules de mâles dans huit nids. Chaque cavité d'arbre était entièrement remplie de rayons.

Minimum nest age (years) [b]	Total comb area (cm^2)	Drone comb	
		Area (cm^2)	Percentage of total comb area
1	22,600	2,300	10.0
2	13,000	2,130	16.4
4	25,800	3,280	12.7
1	26,500	5,350	20.2
1	29,900	5,100	17.6
1	15,600	3,770	24.2
3	20,200	3,740	18.6
2	33,600	5,330	15.9
Mean	23,400	3,880	17.0
± SD	±6,800	±1,240	±3.0

[a] We counted only brood nest combs composed of drone cells as drone comb.
[b] We aged nests through the observations of each bee tree's owner. This gave us minimum nest ages.

TABLE IV. — Patterns of comb use in eight nests. Percentages express the fraction of a nest's total comb area devoted to a cell type-cell function combination. Colonies were thriving when collected. Each nest's cavity was filled with combs.

TABLEAU IV. — Modalités d'utilisation des rayons dans huit nids. Les pourcentages indiquent les fractions de surface de rayon utilisées dans les diverses combinaisons de type et de fonction des alvéoles. Les colonies étaient prospères lorsqu'elles ont été récoltées. Chaque cavité d'arbre était entièrement remplie de rayons.

Collection date	Total comb area (cm^2)	Worker cells [a]			Drone cells		
		% Brood	% Food	% Empty	% Brood	% Food	% Empty
28/July/75	22,600	22	57	11	4	1	5
29/July/75	13,000	24	53	7	0	16	0
30/July/75	25,800	35	25	27	5	0	8
31/July/75	26,500	19	54	7	10	10	0
20/Aug/75	29,900	17	49	16	1	11	6
26/Aug/75	15,600	13	40	23	8	11	5
28/Aug/75	20,200	13	47	21	5	9	5
29/Aug/75	33,600	22	49	13	2	7	7
Mean		20.6	46.7	15.6	4.4	8.2	4.5
± SD		±7.4	±9.8	±7.7	±3.2	±4.9	±1.9

[c] We considered all cells not drone cells as worker cells. We counted only cells in the brood nest with drone cell dimensions as drone cells.

little (SD 3 %) about the mean of 17 %. Construction of drone comb is inversely related to the amount already constructed (FREE, 1967; FREE and WILLIAMS, 1975). Our data indicate this negative feedback regulates the percent drone comb in a nest rather than the absolute amount.

Table IV shows the patterns of comb use in eight nests. Here again we counted only cells of the brood nest with drone cell dimensions as drone cells. For brevity, all other cells are called worker cells in table IV. Although the pattern of comb use varied among nests, a general trend in comb area allocation emerged : 55 % food, 25 % brood and 20 % empty. This predominant devotion of comb to food storage underscores the honey bee's need to store large quantities of honey to survive temperate zone winters.

3. Additional information.

Colony population. Table V lists the worker and drone populations for six colonies. Previous investigators measured the maximum populations of hived colonies and found the following averages : 32,000 (NOLAN, 1925; date interpreted by SIMPSON, 1969), 42,000 (FARRAR, 1937), 45,000 (MOELLER, 1961) and 27,000

TABLE V. — Worker and drone populations of six colonies.

TABLEAU V. — Les populations d'ouvrières et de mâles dans six colonies.

Collection date	Colony condition	Population		Percent drones
		Workers	Drones	
28/July/75	Thriving	23,000	543	2.3
31/July/75	Thriving	23,000	1,154	4.8
26/Aug/75	Thriving	20,000	1,899	8.6
28/Aug/75	Dying	1,000	21	2.1
31/Aug/75	Thriving	14,000	975	6.5
31/Aug/75	Thriving	9,000	453	4.8
Mean		15,000	841	4.8
± SD		±8,600	±602	±2.4

(SIMPSON, 1969). The average population for the six colonies in table V is approximately 16,000. However, direct comparison between the average colony population derived from our data and the preceding figures is invalid. Our data do not record maximums in colony populations. Still, the large differences between the results of the present and previous studies suggest the feral colonies we observed had smaller populations than the hived colonies studied by the earlier investigators.

Honey storage. Table VI shows the amount of honey found in nine colonies. The mean, 13.4 kg, is close to EDGELL's (1949) estimated average of 8.5 kg based on his collection of 56 bee tree colonies. However, feral honey bee colonies may occasionally store far greater quantities of honey. EDGELL's record was 44 kg from a single nest. PERCIVAL (1954) reports harvesting over 200 kg from one feral colony.

TABLE VI. — Honey stores of nine colonies.

TABLEAU VI. — Les dépôts de miel dans neuf colonies.

Date nest collected	Colony condition	Honey (kg)
28/July/75	Thriving	21
29/July/75	Thriving	16
30/July/75	Thriving	16
20/Aug/75	Thriving	26
26/Aug/75	Thriving	10
28/Aug/75	Dying	0
29/Aug/75	Thriving	21
31/Aug/75	Thriving	0
31/Aug/75	Thriving	11
Mean ± SD		13.4 ± 8.6

4. Nest evolution.

MICHENER (1964) has already described nest evolution among bees in general. We examine here the evolution of the *Apis mellifera* nest on a finer scale, within the context of the genus *Apis*. Differences in communicative dances (LINDAUER, 1956), gravity orientation (JANDER and JANDER, 1970) and chromosome number (THAKAR and DEODIKAR, 1966) indicate that *A. florea* and *A. dorsata* are more ancestral than *A. mellifera*. Therefore comparison of the *A. mellifera* nest to the nests of *A. florea* and *A. dorsata* should reveal the advances in nest biology achieved by *A. mellifera*. *A. cerana* was not included in the comparison for lack of data.

The salient characteristics of *A. florea, A. dorsata* and *A. mellifera* nests are listed in table VII. This table is based on the studies of BENTON (1896), RAHMAN and SINGH (1946), LINDAUER (1956), RUTTNER (1968 *a*) and SAKAGAMI and YOSHIKAWA (1973) for *A. florea;* those of BENTON (1896), GRASSÉ (1942), RAHMAN and SINGH (1946), KALLAPUR (1950), LINDAUER (1956), SINGH (1962), RUTTNER (1968 *a*) and MORSE and LAIGO (1969) for *A. dorsata;* and the present study for *A. mellifera.*

Difference in nest site is the pivotal difference between the nest of *A. mellifera* and the nest of *A. florea* or *A. dorsata. Apis mellifera* nests, inside tree cavities, enjoy better thermal insulation and simplified defense relative to the open air nests of *A. florea* or *A. dorsata.* But with these advantages came greater complexity in nest construction. Nest site preparation was added to the nest building sequence. Propolis became a major building material. The multiple

TABLE VII. — Comparisons of *Apis* honey bee nests.

TABLEAU VII. — Comparaisons entre nids d'abeilles du genre *Apis*.

Nest character	*Apis florea*	*Apis dorsata*	*Apis mellifera*
1. Location	Twig of shrub or small tree	Upper limbs of trees	Tree hollows, caves
2. Exposure	Exposed to sun, wind and rain	Exposed to sun, wind and rain	Little exposed to sun, wind and rain
3. Defense features	Sticky ant barriers on substrate branch	Sometimes aggregated nests	Small entrance
4. Nest site preparation	None	None	Rotten wood scraped off cavity walls
5. Construction materials	Wax, propolis, salivary secretion	Wax, propolis, salivary secretion	Wax, propolis, salivary secretion
6. Propolis use	Ant barriers on substrate branch	Coating foreign objects	Propolis envelope, reinforcing combs, entrance smoothing
7. Number of combs	One	One	Several
8. Nest shape	Oval and planar, enlarged top region	Semicircular and planar	Cylindrical, elongate
9. Comb attachment	Comb top surrounds substrate branch	Continuous along top of comb	Intermittent along comb top and sides
10. Nest organization	Honey above, brood below, pollen between; drone comb at bottom	Honey above, brood below, pollen between; no drone comb	Honey above and peripheral, brood centralized and below, pollen between; drone comb peripheral to brood nest
11. Total comb area (cm^2) :			
Max.	1,200+	17,000+	40,000+
Mean	800	9,000	20,000
12. Total cell number :			
Max.	11,000+	60,000+	100,000+
Mean	8,000	32,000	50,000
13. Average cell dia. (wall-wall) × depth (mm × mm) :			
worker cell	2,87 × 7.53	5.42 × 16.87	5.2 × 11.0
drone cell	4.45 × 10.51	lacks drone cells	6.2 × 12.5
14. Honey stores (kg) :			
Max.	2+	25+	100+
Mean	0.25	4	13

comb nest evolved to fit needed comb area into a limited size cavity. And a new nest structure, the peripheral gallery, was developed to aid circulation of bees about these nests with wall-to-wall combs.

The other differences among *Apis* nests appear to be less directly rooted in the change in nest site. The increased honey stores of an *A. mellifera* nest are an adaptation to cold, flowerless winters in temperate regions. And the differences in cell size and number reflect the still poorly understood divergences in the population ecologies of the *Apis* species.

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