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Nest sites of feral honey bees in California, USA

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Summary — Nest site characteristics are described for 94 honey bee nests in trees, 17 in the ground, and 82 in man-made structures. Nests were in trees of mean diameter 85 cm primarily in live hardwoods, especially oaks. Entrances were mostly single knots or cracks in the main trunk at ground level and up to a mean height of 2.5 m. Most nests in the ground were in treeless areas; half had partially exposed combs, possibly aiding ventilation. Nests in buildings differed from those in trees by having smaller entrances. Compass orientation of comb in natural nest sites was commonly from 145° – 195°.

Apis mellifera / feral colony / nidification / nest site

INTRODUCTION

The natural nesting sites of honey bees (*Apis mellifera* L) in the USA have only recently been studied in detail. Avitabile *et al* (1978) analyzed characteristics of 108 "bee trees" in Connecticut. Seeley and Morse (1976) described 39 tree nesting sites in New York, including details of the cavities and combs of 21 of these. Taber (1979) monitored 21 feral colonies in central Arizona over a period of 5 years. We describe here site characteristics of 94 nests in trees and 17 in the ground in California, encompassing a much wider geographic area and variety of habitats than in previous studies. We include data on an additional 82 feral colonies nesting in arti-

cial structures. Our information was gathered while we collected feral bees for a morphometric study which will be described elsewhere.

MATERIALS AND METHODS

The locations of feral colonies in natural sites and artificial structures in 25 counties of California were relayed to us through personal contacts and in response to letters sent to land managers throughout the state. Most of the nests in trees were in park, rural, and wildland habitats. The sample was biased to include nests near human activity and within sight of observers on the ground. We made observations while bees were active during our sampling visits to the entrances of 73 nests in natural sites and 32 in artificial structures. Data on an addi-

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tional 38 natural and 50 artificial sites were provided with bee samples sent to us by project co-operators. As much of the following data as possible was gathered for each colony: date of observation; county; locality; identity of tree (family and genus) and diameter at breast height (dbh, at 1.6 meters) for tree nests; shape and area of opening (dimensions of the opening were measured and the area of the regular polygon most closely approximating the shape of the entrance was computed); height of the bottom of the entrance above ground; compass orientation of entrance (magnetic north = 0°); and compass orientation of combs (the long comb axis when viewed from above).

Nest cavities were not opened and incomplete data were obtained for some nests. Nests with multiple openings (5 from trees and 2 from buildings) were excluded from analysis of entrance height, area, and orientation. Nest types were classified as tree, ground, or artificial to allow comparison of site characteristics between these categories. For ground nest entrance height comparisons, only the subset of nests in cliffs or vertically oriented surfaces was considered.

Since distributions were irregular, median and mode are included with descriptive statistics. Significance values for comparisons among entrance areas (of less than 1000 cm²), entrance heights, and tree dbh are based on the Kruskal-Wallis H statistic corrected for ties and compared to the χ^2 distribution. Statistical analyses were performed with SPSS^x (Anonymous, 1986), except for directional nest entrance orientation and comb orientation data, analyzed using Rayleigh's test (Batschelet, 1981).

RESULTS

Nests in Trees

Of 94 nests in trees, all but 6 were in living trees. We were able to identify the genus of the host tree for 82 nests; 1 colony was found in a palm tree of unspecified genus; and 11 were from unidentified live or dead trees (table I). For the 82 colonies, we collected information on tree size from 51

(fig 1), height of entrance from 50 (fig 2), entrance size from 40 (fig 3), location (base, trunk, limb) and type of entrance (knot, crack) from 37 (table II), compass orientation of entrance from 44 (fig 4), and orientation of combs from 7 (fig 5).

Most entrances (32 of 37, or 86%) were located on the trunks of trees. Of the 32 entrances, 24 were on the main trunk (12 at knots; 12 at cracks) and 8 at the base of the tree (6 openings wider than high; 2 at vertical cracks). Five nests on limbs were at the stubs of broken limbs (4) or at a knot (1). One additional colony was not in a cavity, but constructed in the space between the trunk and hanging fronds of a date palm (*Phoenix*) tree.

Nests in the ground

Seventeen colonies were in cavities or shallow recesses in the ground (6) or cliff faces (11). Of the 13 visited, 3 had entrances on fairly level ground, 8 had openings in vertical or steep cliffs, and 2 in cliffs had mostly exposed combs. Twelve of the colonies visited were in desert areas with trees either absent or sparse; the remaining colony was in a coastal coniferous forest. We measured the entrance area of 10

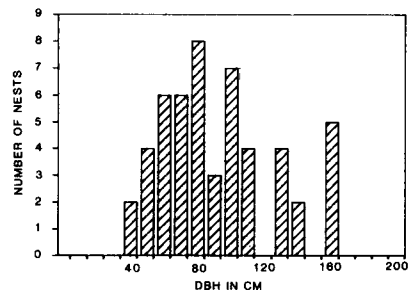


Fig 1. Distribution of tree dbh (cm) for 51 nests. Mean = 85.59; sd = 33.57; median = 76; mode class = 70-80; range = 38-152.

Table I. Trees occupied by nesting feral colonies *.

<i>Family</i>	<i>Genus</i>	<i>Common Name</i>	<i>Number of colonies</i>
Fagaceae	<i>Quercus</i>	Oak	43
Myrtaceae	<i>Eucalyptus</i>	Gumtree	10
Platanaceae	<i>Platanus</i>	Sycamore	8
Anacardiaceae	<i>Schinus</i>	Peppertree	5
Cupressaceae	<i>Cupressus</i>	Monterey Cypress	4
Lauraceae	<i>Umbellularia</i>	Bay	2
Leguminosae	<i>Robinia</i>	Black Locust	2
Ulmaceae	<i>Ulmus</i>	Elm	2
Bignoniaceae	<i>Catalpa</i>	Catalpa	1
Oleaceae	<i>Olea</i>	Olive	1
Palmae	<i>Phoenix</i>	Date Palm	1
Palmae	unspecified	"palm"	1
Tamaricaceae	<i>Tamarix</i>	Tamarix	1
Moraceae	<i>Morus</i>	Mulberry	1
Agavaceae	<i>Yucca</i>	Joshua Tree	1
Unidentified			11

* Family names according to Bailey and Bailey (1976).

nests (fig 3), orientation of entrance of 9 (fig 4), orientation of combs of 4 (fig 5), and entrance height of 8 cliff nests (fig 2). Of the four not visited, 2 were reported from crevices in a rock or cliff, 1 was dug from the ground, and 1 was found in a brush pile.

Nests in artificial structures

Eighty-two colonies were reported from various types of artificial structures, most often in buildings (62, or 76%). Colonies in the latter were found in an attic, eaves, a light fixture, under the roof, in vent fans, and within walls. The space between walls was the most frequent location for nesting sites in buildings (41 out of a total of 62, or 66%). In other artificial structures, nests

were found under a doghouse, in wood duck nesting boxes, a barbecue, a tractor, a food locker, a packing crate, an ice box, an abandoned beehive, and in various pipes and housings for pumps, wells, and exhaust systems associated with irrigation systems or with oil-field machinery.

We measured the height of entrance for 16 nests in buildings (fig 2). For nests in buildings and other structures, we measured the entrance size of 19 nests (fig 3), the compass orientation of entrance of 23 nests (fig 4), and comb orientation of 5 nests (fig 5).

Height of nest entrance

The 3 distributions of height of nest entrance in trees, buildings, and cliffs were

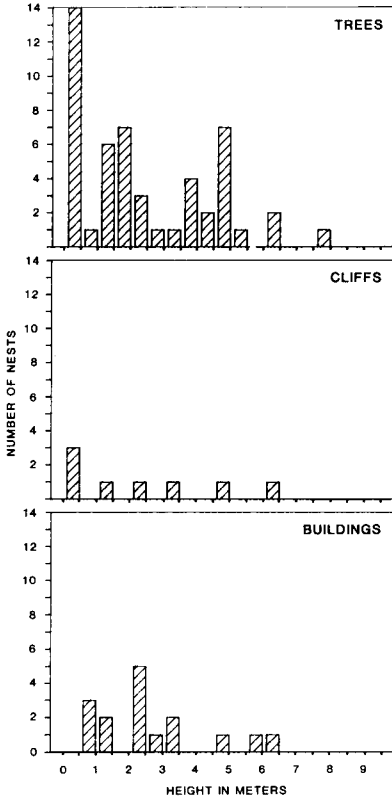


Fig 2. Distribution of height (m) of entrance from ground level to bottom of nest entrance for: 50 tree nests (mean = 2.28; sd = 2.05; median = 1.53; mode class = 0–0.5; range = 0–7.63), 8 nests in cliffs (mean = 1.34; sd = 2.15; median = 1.86; mode class = 0–0.5; range = 0–6.10), 16 nests in buildings (mean = 2.64; sd = 1.61; median = 2.46; mode class = 2.0–2.5; range = 0.62–6.15).

not different (fig 2; $\chi^2 = 1.23$; df = 2; $P > 0.05$). Mean height of entrances in 50 trees was 2.5 m. Some entrances were at ground level, but most were above (42, or 84%). Height of opening did not differ among the 3 most frequent genera of trees ($\chi^2 = 3.32$; df = 2; $P > 0.05$). Above 5 m the frequency of nest entrances diminished. This may reflect not only the de-

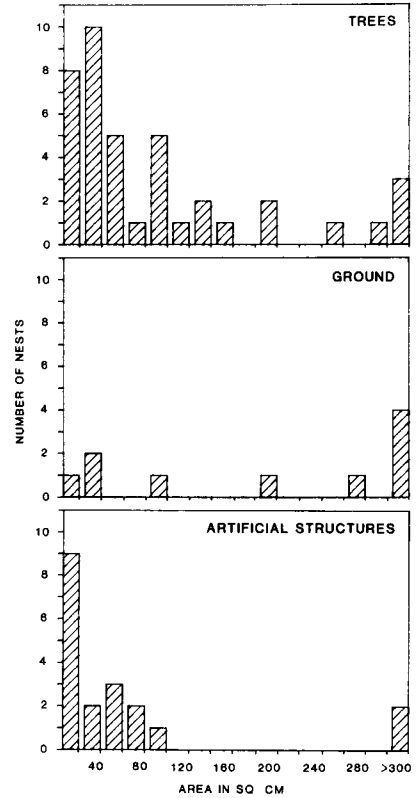


Fig 3. Distributions of nest entrance areas (cm²) of: 40 tree nests (mean = 110.30; sd = 177.62; median = 46; mode class = 20–40; range = 2–972), 10 ground nests (simple statistics computed on 9 nests after excluding maximum value of 4560; mean = 285.7; sd = 303.13; median = 182; mode class = 20–40; range = 8–900), 19 artificial structures (mean = 102.68; sd = 229.34; median = 24; mode class = 0–20; range = 1–929).

creased size of trunks and limbs, but also increased difficulty in discovering nests higher on trees.

Mean entrance height for 16 nests in buildings was 2.6 (fig 2). Nests in upper stories of multi-story structures might be under-reported because of reduced visibility. Ground-nesting colonies were most of-

Table II. Comparison of host tree characteristics. Percentages and statistics often computed on less than total number of nests examined; nr = not reported.

<i>Characteristic</i>	<i>This study</i>	<i>Seeley & Morse (1976)</i>	<i>Avitabile et al (1978)</i>
Total nests	94	39	108
Number of host genera	14	16	12
Most common	<i>Quercus</i> (52%)	<i>Acer</i> (33%)	<i>Quercus</i> (20%)
Second	<i>Eucalyptus</i> (12%)	<i>Quercus</i> (25%)	<i>Juglans</i> (13%)
Hardwoods	92%	94%	83%
Conifers	5%	6%	17%
Monocots	4%	0	0
Live trees	94%	94%	75%
Single entrance	94%	90%	79%
Tree dbh in cm:			
Mean	85	nr	90
Range	38–152	nr	30–180
Primary entrance on			
Trunk and base	86%	nr	72%
Limbs	14%	nr	28%
Primary entrance at			
Knots or stubs	46%	56%	69%
Cracks	32%	32%	30%
Base or roots	22%	12%	1%
Entrance height in m			
Mode class	0–0.5	0–1	2–3
Median	1.5	1–2	3–4
Entrance area in cm ²			
Mode class	20–40	10–20	35–40
Median	46	20–30	60–65
Most frequent orientation of			
Entrance	Random	Random	225°
Combs	145°–195°	Random	nr

ten associated with openings in vertically oriented surfaces. Mean entrance height for 8 nests in cliff faces was 2.2 m (fig 2).

Entrance area

The distributions of areas of nest entrances for nests in trees and artificial structures were variable and roughly bimodal: small

openings less than 100 cm², or very large openings resulting in semi-exposed nests (fig 3). Entrance area varied significantly according to the type of site ($\chi^2 = 6.55$; $df = 2$; $P < 0.05$). Openings into artificial structures were mostly cracks or small holes with a median of 24 cm². Some entrances were just large enough for a bee to enter. The entrances in trees had a larger median of 46 cm² and were not different

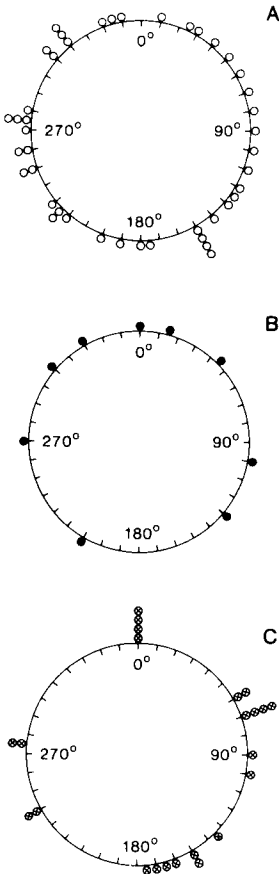


Fig 4. Compass orientation (0° = north) of nest entrance of A) 44 tree nests; B) 9 ground nests; C) 23 nests in artificial structures.

among the 3 most frequent genera of trees ($\chi^2 = 5.49$; $df = 2$; $P > 0.05$). Entrances in ground nests were often poorly defined and measurement was approximate.

Orientation of nest entrance

No directional bias of entrance orientation was detected for tree (Rayleigh's $Z = 0.29$,

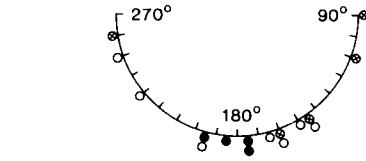


Fig 5. Compass orientation of comb (long axis) for 7 nests in trees (open circles), 4 ground nests (solid circles), and 5 nests in artificial structures (circles with crosses).

$P > 0.10$, $n = 44$), ground ($Z = 0.69$, $P > 0.10$, $n = 9$), or artificial ($Z = 1.78$, $P > 0.10$, $n = 23$) nest sites (fig 4).

Orientation of comb

We measured comb orientation at 13 colonies in natural situations (tree and ground cavities) and 5 colonies in artificial structures. Two of the colonies in natural situations had variable comb orientations, and were excluded from our analysis. Unlike orientation of nest opening, which is unidirectional and can vary throughout 360 degrees, comb orientation is axial and can be uniquely described within any 180 degrees of arc. We express comb orientation as a value between 90° and 270° ($180^\circ =$ north-south axis) to best illustrate our findings (figure 5). Data pooled from all samples (trees, ground and artificial structures) show a uniform (or random) comb orientation distribution ($Z = 1.69$, $P > 0.10$, $n = 16$), as do the data from artificial sites alone ($Z = 0.49$, $P > 0.10$, $n = 5$). There were too few ground nests for statistical evaluation, so data from natural sites (ground and tree nests) were pooled; comb orientation for this set was non-uniform ($Z = 3.54$, $P < 0.025$, $n = 11$), with a mean angle of 184° .

The 2 colonies in natural situations with variably oriented combs were both largely exposed. One was the colony built on the date palm (*Phoenix*) tree, in the space between the trunk and a dense shield of hanging dead fronds. Vertical combs (at least 8) were attached to the trunk in a radial arrangement, so that the space between combs at the trunk was less than between the outermost comb portions nearest the fronds. Comb orientation varied from 55° to 120°. The second set of variably oriented combs was in an abandoned nest in a cavity in a vertical cliff. Ten combs were oriented at 210° and 3 were oriented at 245°.

DISCUSSION

Honey bees do not enlarge their nest cavity except to clean and prepare the interior surface of the enclosure. They must make use of pre-existing cavities of either natural or man-made origin. We examined colonies from urban and agricultural areas, and from nature reserves in coastal regions, inland valleys, deserts, foothills, and mountains. Of nest sites in trees, 76 out of 83 (92%) in our study, and most of those reported by others (table II), were in cavities in the trunks of live hardwood trees. In California, the only conifer selected by bees, Monterey Cypress, *Cupressus macrocarpa*, had 4 out of 83, or 5% of nests. This species has been planted extensively along the coast of California (Griffin and Critchfield, 1976). Three nests, including the exposed nest, were in monocot trees.

Bees used hardwood trees in 11 families and genera for nest sites, with 85% of all tree nests in just 5 genera (table 1). Hardwoods in California are estimated to occupy 5–6 million hectares (12–15 million acres) and account for roughly 26% of the total wood volume of California's forests

(Pillsbury and Kirkley, 1984). Oaks, *Quercus* spp., were hosts to 52% of colonies in trees. This genus was also among the favoured trees reported elsewhere, but at lower frequencies (table II). Oaks are usually dominant in California hardwood communities (Griffin and Critchfield, 1976).

Bee trees reported here and elsewhere are similar in diameter when measured at 1.3–1.6 m height: minimum, 30–38 cm, and mean, 85–90 cm (table II). Since bees will only make use of cavities larger than about 10 litres (Rinderer *et al*, 1981; Seeley, 1977), suitably large cavities are unlikely to be found in young trees or those with small diameters. Likewise, the inverse relation between tree diameter and height results in the more likely occurrence of suitable cavities at lower heights. In our sample of 50 tree nests the median entrance height was 1.5 m. Since the entrance is usually near the nest cavity (Seeley and Morse, 1976) these data would indicate that in California, the majority of suitable tree cavities are close to the ground. Seeley and Morse (1976) also found a predominance of entrances at or near ground level in New York State, as did Taylor and Otis (1978) for Africanized honey bees in French Guiana. However, Seeley and Morse (1978) found that when bee swarms were offered identical trap boxes 1 m and 5 m high they preferred to occupy the higher one. Lacking a means of detecting nests equally well at all heights, we cannot determine the extent to which sampling bias (nests nearer to the ground are easier to detect) affected our measure of nest height distribution.

We found no preferred orientation of the nest entrance, but Avitabile *et al* (1978) found a predominance of SW facing openings (table II).

Certain features of artificial nest sites were different from those of natural ones. Comb orientation appeared to be more

variable than in natural sites, but our sample was small. Entrances into buildings were smaller than those in trees, with means of 30.3 cm² and 69.0 cm², respectively. Although the entrance heights in buildings were not statistically different from those in trees, we found no entrances at ground level in buildings.

The hot, arid climate and treeless regions of the Southern interior of California would appear to be inhospitable to European bees, yet feral colonies are not totally excluded from even the most barren habitats. Our observations of thriving colonies in deserts are evidence that a proper combination of cavity, exposure, shade, and access to water can create favourable microhabitats for colonies. Furthermore, natural food and water resources are supplemented by irrigation of agricultural and residential developments, thus encouraging colonization of the desert by feral bees.

Twelve of the 13 ground colonies visited were in desert or treeless areas. Without a mantle of soil and vegetation, deserts may have a high frequency of suitable ground cavities. Taber (1979) found 20 colonies in cavities in limestone cliffs within a 1 km radius. In our study partial exposure of combs in ground nests was more frequent than in trees: 7 of the 13 ground colonies (54%) had the combs visible from the entrance, as opposed to 8 out of 62 (13%) in trees. In addition, openings in the ground were more often larger: only 4 out of 10 ground nests had entrances 100 cm² or smaller, compared with the median value of 46 cm² for tree nests. However, even the most fully exposed ground nests were partly tucked into crevices. Taber (1979) also noted exposure of combs in half of the ground-nesting colonies he described in central Arizona. While such exposure might be explained simply as the growth of the colony beyond

the capacity of the cavity or the lack of suitable cavities, it may also facilitate ventilation.

Our observation of the general north-south arrangement of natural combs supports the report of De Jong (1982; but see Ifantidis, 1978; Taylor and Otis, 1978) that bees use the earth's magnetic field for orientation of combs.

Among the colonies we visited were some that were large, vigorous, and at sites that had apparently been occupied for more than a year. Although our collecting methods stimulated mild defensive behaviour by the bees and we occasionally smelled alarm pheromone, we experienced few instances of stinging behaviour. The strongest responses were associated with our attempts to cut away the comb or when we blew into the entrance to increase the activity of bees. None of the colonies examined displayed the intense defensive behaviour ascribed to Africanized bees (Collins *et al*, 1982).

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Résumé — Sites de nidification des colonies sauvages d'abeilles (*Apis mellifica*) en Californie, USA.

Les caractéristiques des sites de nidification sont décrites pour 193 nids d'abeilles répartis dans 25 districts de Californie. 94 nids se trouvaient dans des arbres, 17 sur le sol et 82 dans des structures créées par l'homme. Les données recueillies ont porté sur la taille, la hauteur et l'orientation de l'entrée du nid et sur l'orientation des rayons. Pour les nids trouvés dans les arbres, l'espèce botanique et la taille de l'arbre ont été ajoutées.

94% des nids situés dans les arbres se trouvaient dans des arbres vivants, 92% dans des feuilles et 52% dans des chênes (*Quercus*) (tableau I). Les trous de vol étaient le plus souvent de simples noeuds ou fissures dans le tronc principal, au niveau du sol et jusqu'à 2,5 m de haut en

moyenne. Le diamètre moyen de l'arbre à 1,6 m était de 85 cm (fig 1), le diamètre minimum de 38 cm et il est peu vraisemblable que des arbres moins gros soient capables de former des cavités suffisamment grandes pour être occupées par une colonie d'abeilles.

Les nids dans le sol étaient la plupart du temps situés dans des zones sans arbres et associés à des surfaces plus ou moins verticales. La moitié d'entre eux avaient des rayons partiellement à l'extérieur, peut-être pour faciliter la ventilation. L'entrée des nids étaient souvent mal définie.

Les bâtiments représentaient 76% des structures artificielles qui hébergeaient des colonies d'abeilles. 66% des colonies nidifiant dans des bâtiments occupaient l'espace entre les murs. Dans ces cavités artificielles, les ouvertures conduisant au nid étaient significativement plus petites que dans les cavités naturelles (fig 3). La hauteur du trou de vol ne différait pas significativement d'une catégorie de nids à l'autre. La moyenne générale était de 2,25 m avec une valeur médiane de 1,86 m (fig 2). L'orientation du trou de vol était aléatoire pour toute les catégories de nids (fig 4). L'orientation des rayons dans les cavités naturelles ne l'était pas : l'axe magnétique nord-sud était privilégié (orientation moyenne : 184°) (fig 5).

Apis mellifica / colonies sauvages / nidification / site de nidification

Zusammenfassung — Nistplätze von wildlebenden Bienenvölkern in Kalifornien. Für die Nistplätze von 193 Bienenvölkern in 23 Bezirken Kaliforniens werden die bezeichneten Eigenschaften beschrieben. 94 Nester befanden sich in Bäumen, 17 im Erdboden und 82 befanden sich in von Menschen errichteten Strukturen. Es wurden Daten über Größe,

Höhe und Himmelsrichtung des Flugloches sowie über die Orientierung der Waben gesammelt. Für die Nester in Bäumen wurde die Baumart bestimmt sowie die Größe des Baumes notiert.

Von den Baumnestern befanden sich 94% in lebenden Bäumen, 92% in Laubbäumen und 52% in Eichen (*Quercus*; Tabelle I). Als Flugloch wurden einzelne Astlöcher oder Risse im Hauptstamm, von Bodenhöhe bis zu einer mittleren Höhe von 2,5 m benützt. Der mittlere Durchmesser der Bäume in einer Höhe von 1,60 m betrug 85 cm (Abb 1). Der kleinste Durchmesser betrug 38 cm; es ist unwahrscheinlich, daß noch kleinere Bäume Höhlen bilden können, die zur Aufnahme eines Bienenvolkes ausreichend groß sind.

Die meisten der Bodennester befanden sich in baumlosen Gegenden mit sehr steilen Erhebungen. Viele hatten teilweise exponierte Waben, möglicherweise zur Erleichterung der Ventilation. Die Eingänge zu den Bodennestern waren oft nur ungenau markiert.

Eine Vielfalt künstlicher Strukturen beherbergte Bienenvölker. Gebäude waren am häufigsten (76%); von den Völkern in Gebäuden hatten sich 66% in dem Zwischenraum zwischen den Hauswänden angesiedelt. Die in den künstlichen Strukturen zur Nisthöhle führenden Eingänge waren viel kleiner als die Fluglöcher von natürlichen Höhlen (Abb 3).

Die Höhe der Fluglöcher über dem Erdboden war bei den drei Nestkategorien nicht signifikant verschieden. Das Gesamtmittel betrug 2,25 m, mit einem Medianwert von 1,86 m (Abb 2). Die Orientierung des Flugloches war für alle Nistkategorien zufällig (Abb 4). Die Orientierung der

Waben in natürlichen Höhlen war nicht zufällig; es wurde deutlich die magnetische Nord-Süd-Achse bevorzugt (mittlere Orientierung = 184°) (Abb 5).

***Apis mellifera* / wildlebende Bienenvölker / Nidifikation / Nistplatz**

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