

The Little Architect with Its Marvellous Creation: A Study on the Nest Architecture of Tropical Hornet, *Vespa affinis*[†]

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Abstract: Knowingly or unknowingly, we are surrounded by many creatures that are specialized in building amazing structures with great finesse. It is really wonderful to see how such tiny brains coordinate with each other to create perfect structures, which is perhaps impossible for humans. On similar lines, the present study describes the nest architecture of tropical hornet, *Vespa affinis*, built across several locations in Jalpaiguri district of West Bengal, India. Mature nests are roughly pear shaped, broadening from the top to the truncate base. The architecture of the nest is in the pattern of a spiral staircase with a central and several auxiliary petioles supporting each of the comb layers. Two large usually round entrance holes along with 6-7 small holes were also seen on the walls of the nest. Strikingly, the hypertrophy of the nest envelope above the combs into a prominent roof cone with cellular structure is observed. The hardening of the nest texture and the extensive papering over of the cells in the initial comb layers, thereby reducing their reutilization, form an essential feature of the nest. Several morpho-metric measurements of a typical nest (with seven comb layers) from the study site was conducted. Each comb layer of the nests showed a rough bimodality of cell diameter, with peaks at about 0.85 and 1.0 mm. The maximum number of occupied cells in the centremost stages of the nest (i.e., comb layer 3) probably support the maximum number of brood members. The highest number of auxiliary petioles along with the tree branch provide the greatest protection to the brood in this layer. Besides the highest number of petioles, the maximum number of unoccupied cells in comb layers 2 and 4 also provide extra protection to the developing brood in the comb layer 3. A decrease in the rate of nest building in the final stages (i.e., comb layers 6 and 7) is evident by the decrease in the number of cells in these layers.



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1. Introduction

Animal architecture is a less debated topic of animal behaviour. It elaborates not only a balance between the usage of cheap and durable materials but also reflects the builder's capacity to design a perfectly engineered structure. Such construction also reflects the utilization of division of labour while maintaining the necessary style and intricate design.

The nest of *Vespine* species commonly known as true hornets has been observed by workers in the vast regions of Asia, Europe and North America [1–5]. Although different species of *Vespine* wasps have been reported worldwide, *Vespa affinis* has been found to be distributed exclusively in and around the Indo-Malayan Peninsula.

Hornets produce pear-shaped nests to support their large colonies. These nests are built at a sufficient height above the ground and consist of several parallel combs joined by supporting petioles. There is a rough bimodality in the measurement of cell diameters of the combs of each nest. Although a large proportion of cells in each of the comb layers are

used to rear a single generation of wasps, combs used to rear a second and rarely a third brood are also found [6].

A preliminary study of significance on the nature and the structure of the nest of *Vespa affinis* has been performed by workers in the Indo-Malayan region [7–11], but a detailed description of the nest architecture is still lacking. In this paper, we emphasize the various parameters required to construct a perfect nest by the tropical hornets, *Vespa affinis*.

2. Methodology

Field observations of the nests of *Vespa affinis* were made across different locations in Jalpaiguri district (26°16'–27°0' N latitudes and 88°4'–89°53' E longitudes), West Bengal, India, during 2022. Nests from mature colonies were observed hanging mostly from the shrubs in the study area. Nests were also found attached to the walls in the surrounding area. A nine-month-old, abandoned nest supporting a mature colony was removed in order to study its detailed architecture. All our observations were compared with those obtained from some old nests of mature size.

For the sake of the study, all combs in the nests at the study site were numbered from the top, so that comb 1 is the earliest and uppermost in the nest. The number of cells, mean cell diameter and subsequently the area and volume of the individual cells in each comb layer were determined. The cell diameter measurement used here is between the opposite sides of the cells rather than the opposite corners. Each of the cell diameter measurements is the mean from at least one row of 8–10 cells. The distance between the adjacent comb layers, angles between them and the number of connecting petioles were also noted. The volume of the entire nest was determined using the formula, $1/3 \pi r^2 h$, by considering the entire nest to be a cone. The basal area of the entire nest and the height of the entire nest including the roof cone was measured using a measuring tape. The cell diameter of the hexagonal cell was used to calculate the area of a complete hexagon (a summation of the areas of two trapeziums). The volume of the hexagonal cell was determined using the formula, $\pi r^2 h$, by considering each cell to be a complete cylinder. The number of capped and uncapped cells in each of the comb layers was counted. The interior angles of the centrally situated occupied and peripherally situated unoccupied cells were also counted. All the measurements were performed using a graduated ruler, set square and protractor. A cell with a cocoon or a faecal pellet was recorded as having been utilized to rear at least one wasp. To estimate the number reared per cell, we took the standard approach [12] of dissecting a sample of cells and counting the number of faecal pellets.

3. Results

The following description of the entire nest of *Vespa affinis* is based on the study of seven nests obtained from the study area. In most cases, the nest substrate was a single tree branch, but other nests in fairly dense vegetation with several branches or twigs running through them were also observed. The nests in the study area were mostly built on *Ixora* sp and *Hibiscus* sp shrubs. Single nest was located attached to the wall. All these nests were observed at a height of more than 1.5 m above the ground. Mature nests are roughly pear shaped, broadening from the top to the truncate base (Figure 1).

The architecture of the nest is in the pattern of a spiral staircase with a central and several auxiliary petioles supporting each of the comb layers (Figure 2).

The number of supporting petioles increases with each layer, maximizes at the central layer and again decreases at the comb layers in the nest. The distance and the angles between the individual comb layers vary with each layer (Table 1) (Figure 3a,b).



Figure 1. Entire nest of *Vespa affinis*.



Figure 2. Spiral staircase pattern in the nest architecture of *V. affinis*.

Table 1. Number of petioles, distance and the angle between each comb layer.

Comb layer	Number of Petioles between Each Comb Layer	Distance between the Comb Layers (cm)	Angle between the Comb Layer
Between comb layers 1 and 2	1 central	1.26	28°
Between comb layers 2 and 3	1 central and 6 auxiliary	1.7	36.5°
Between comb layers 3 and 4	15 auxiliary including single tree branch	2.72	11°
Between comb layers 4 and 5	6 auxiliary including single tree branch	1.27	2°
Between comb layers 5 and 6	1 central and 3 auxiliary	1.64	8.5°
Between comb layers 6 and 7	1 central	0.88	1°



Figure 3. (a,b): view of connecting petioles in between the comb layers.

Two large usually round entrance holes on the basal edges of the nest were observed. Some nests with 6–7 small holes were also seen on the surface of the walls. Although the wasps were seen entering and leaving through all these holes, only the two larger ones appeared to be the actual entrance holes. One of the striking features of the nest is the hypertrophy of the envelope above the combs into a prominent roof cone. The roof cone has a cellular structure and is hard in texture as compared to the thin covering of the basal layers of the nest (Figure 4).



Figure 4. Cellular structure of roof cone.

Of all the nests studied closely, one had seven combs (Figure 5), with a mean of about 2500 cells and a total comb face area of about 348.48 cm². Although the area of comb layer 5 is the maximum, the comb layer 3 contains the maximum number of occupied cells. The mean height of the entire nest is 38.92 cm (Table 2), and the mean width near the base is about 21.06 cm. The volume of the entire nest was about 4520.98 cc.

Table 2. Height of different nests isolated from the study area.

Number of Comb Layers	Height of Roof Cone (cm)	Height of the Nest below the Roof Cone (cm)
7	13.06	25.86
7	18	36
9	27	60
5	9	14

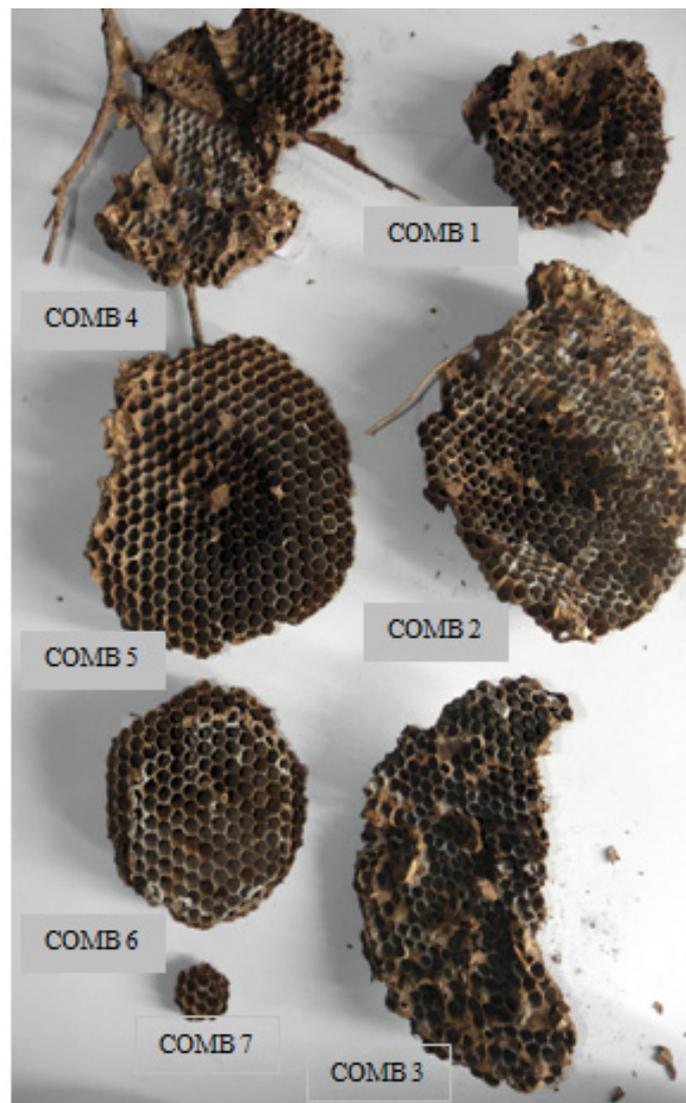


Figure 5. Individual comb layers of the nest of *V. affinis*.

The hexagonal cells of the *V. affinis* do not seem to fall into two clear size types, and it is difficult to distinguish between small-cell and large-cell combs. Measurements from each of the comb layers of the nests showed only a rough bimodality of cell diameter, with peaks at about 0.85 and 1.0 mm. This was also associated with a wide variation in the area and volume of the occupied cells in each comb layer (Table 3). The interior angles of the incomplete hexagonal cells present in the periphery of each comb layer was much greater compared to the angles of the centrally placed utilized hexagonal cells (Table 3). Comb layer 3 was seen to have the maximum number of occupied cells (Figure 6). The closure of the disused cells was observed in each of the comb layers. The maximum percentage of closed cells was noted in the first comb layer containing papered cells that were subsequently sealed with a thick glue-like covering, providing it a hardened texture. Combs 3 and 4 had a large number of closed cells, in spite of being papered and lacking a thick glue-like covering (Figure 6). The subsequent comb layers of cells exhibited a marked decrease in the number of closed cells. Thus, the tendency of reutilization of the cells in the nest of *Vespa affinis* only appears in the later stages of the comb layers. The last comb layer of cells was open and unoccupied and was probably incompletely formed.

Table 3. Morphometric parameters of the nest.

Morphometric Parameters	Comb Layers						
	Comb Layer 1	Comb Layer 2	Comb Layer 3	Comb Layer 4	Comb Layer 5	Comb Layer 6	Comb Layer 7
Number of cells (mean ± SE)	302 ± 1.030	758 ± 1.048	284 ± 1.150	397 ± 0.547	425 ± 0.899	240 ± 0.925	22 ± 0.663
Area of the comb layer (cm ²) (mean ± SE)	131.78 ± 0.60	333.42 ± 1.92	141.82 ± 1.03	269.71 ± 0.81	271.72 ± 0.316	162.86 ± 0.316	13.2 ± 0.034
Diameter of occupied cells (cm) (mean ± SE)	0.89 ± 0.067	0.85 ± 0.054	0.97 ± 0.031	1.1 ± 0.031	1.0 ± 0.0316	1.1 ± 0.0315	1.0 ± 0.0316
Area of occupied cells (cm ²) (mean ± SE)	0.46 ± 0.006	0.46 ± 0.006	0.50 ± 0.008	0.68 ± 0.0077	0.64 ± 0.0078	0.68 ± 0.0077	0.59 ± 0.0088
Volume of occupied cells (cc) (mean ± SE)	1.020 ± 0.03	1.221 ± 0.031	1.929 ± 0.02	1.859 ± 0.025	1.772 ± 0.0200	2.452 ± 0.0325	2.04 ± 0.0316
Interior angles (occupied) (in degrees) (mean ± SE)	129° ± 0.385	121.71° ± 0.32	120.5° ± 0.49	123.3° ± 0.23	128.83° ± 0.23	116° ± 0.391	Nil
Interior angles (unoccupied) (in degrees) (mean ± SE)	149.66° ± 0.3	150.66° ± 0.26	151.5° ± 0.43	154.0° ± 0.49	154.5° ± 0.278	146.75° ± 0.41	150.1° ± 0.26

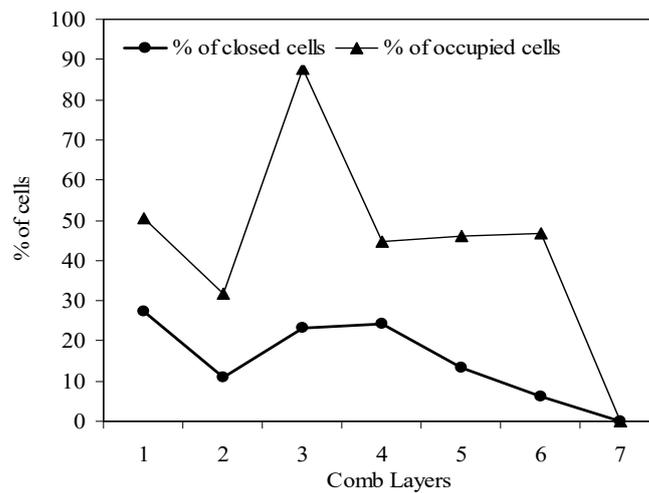


Figure 6. Percentage of occupied and closed cells in each comb layer.

4. Discussion

Insect nest construction and architecture highlights a trade-off between thermoregulation and foraging, keeping in mind the need for survival and maintenance of offsprings [4]. Therefore, nest architecture reflects an extended phenotype of any typical vespine colony [4]. As observed in the present study, the construction of the nest of *Vespa affinis* on the leeward side along with a well-built roof cone reduces its vulnerability in a tropical humid habitat. Besides the hardened texture in the initial stages, the presence of several haphazardly arranged air pockets or incompletely formed cells in between the roof cone and the first comb layer provides protection to the brood rearing cells in the subsequent comb layers. Although under persistent acceleration, the hornets are known to build a perfect nest, maintaining the required geotropism [13]. Importantly, vespine nests are attached by a pedicel to the nest roof cone. Subsequently, nests attain a spherical or ellipsoidal shape and curve upwards at the centremost region. However, the pedicels are long enough and provide an easy pathway for wasps to move from one comb to another within nests [14].

Besides possessing a keystone for the attachment of the cell’s ceiling to the substratum, which is subsequently hardened by saliva [15], the walls and the roof of each comb possess minerals such as ferrites, titanium and zirconium, which are known to reflect infrared light [16]. Importantly, salivary cement is composed of P, Mg, S, Cl, K and Ca [17]. The

ability of extensive papering over of the cells in the initial comb layers and their subsequent closure by mud in layers 3 and 4, thereby preventing their reutilization in *V. affinis*, also increases the durability of the nest. Thus, the solid roof cone and its hardened texture coupled with the ability of *V. affinis* of papering over old cells appear to be characteristic features of the studied nest [18]. The microscopic investigation of the nest material of *V. velutina* revealed the agglomeration of microelements primarily composed of lignocelluloses spatially arranged into alternating bands of brown and beige stripes [4,19]. The presence of bands of different colours in each papered layer, covering the surface above the nest, provides a spectacular view. A similar observation on the nest envelope of *V. velutina* also reveals the presence of a shell-like structure with short air pockets [4,20].

The maximum number of occupied cells in the centremost stages of the above nest (i.e., comb layer 3) supports the maximum number of brood members, providing the greatest possible protection. Observation by [4] on the nests of *V. velutina* revealed the maintenance of the central theme of stability and preservation of optimum brood temperature. The maximum number of auxiliary petioles along with the tree branch provides the greatest degree of protection to the brood in this layer. Similar investigation on the vespine nests by [4] showed the existence of a tree branch along with several secondary tree branches supporting the pear- or spheroid-shaped nests. Besides the greatest number of petioles, the highest number of unoccupied cells in comb layers 2 and 4 also provide extra protection to the developing brood in the comb layer 3. The maximum inclination of comb 3 with respect to comb 2 and its greatest distance from comb 4 also provide additional support to the nest under constant acceleration. In accordance with the present study, the number of petioles, the number of unoccupied cells, a perfect angle of inclination and the greatest distance with respect to comb 3 appear to be the optimum parameters required to build a complete nest with the maximum number of occupied cells. The rate and amount of comb building are moderate in the initial stages of the nest, and they become very high at the intermediate comb layers and gradually decrease in the final two layers. In the present study, the hornets were probably involved in building a nest having a hardened texture up to comb layer 3. This hardness of the nest decreased in the subsequent layers when the hornets were more concerned about increasing the number of cells per layer. This is associated with an increase in the area and volume of the cells per comb layer. The amount and extent of comb building is positively correlated with the number of hornets per group [21]. Researchers [22] have also stated that the nest parameters of *V. velutina*, i.e., weight, height, diameter, number of cells and total number of individuals in the nests are directly related. A high consumption of β -alanine and γ -aminobutyric acid (GABA) in *V. orientalis* was significantly associated with their reduced life span, in turn negatively influencing their nest construction behaviour [23]. Finally, this study also reflects a decrease in the rate of nest building in the final stages (i.e., comb layers 6 and 7) as evident by the abrupt decrease in the number of cells in these layers. This is associated with the decrease in the number of comb-building hornets per group, probably due to their movement away from the nest. This sudden desertion of the nest is perhaps a result of a conscious decision made by the hornets due to the shortage of food or the increase in attacks from predators. The increasing size of the nest probably made the nest more conspicuous, and thus, an easy target for enemies.

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