Formosan Entomologist
Journal Homepage: entsocjournal.yabee.com.tw

【Research report】

# 採自台灣的黑絨虎頭蜂(Vespa basalis)(Hymenoptera: Vespidae)巨型蜂巢【研究報告】

山根爽一

*通訊作者E-mail :

Received: Accepted: 1992/02/07 Available online: 1992/03/01

## Abstract

## 摘要

在台灣中部埔里郊外採集的黑絨虎頭蜂成熟巢，可能是世界記錄最大的虎頭蜂巢。蜂巢卵形，大小(直徑×高)65×95公分，全體被外殼覆蓋，巢頂呈圓錐形。本蜂巢不見於其他種類的蜂巢構造特徵是外殼側面縱向的長形出入口。這巢共有三個出入口，形狀都是長形裂口(1×17公分)。蜂巢之內部有15個圓形巢脾，總計40000多個蜂室。在巢內採集的成蟲數目包括558隻工蜂，579隻雄蜂與535隻后蜂。但在採取蜂巢時，成蟲幾乎全部為工蜂，有相當數目的成蟲逃逸了。估計羽化(含擬蛹與蛹)的工蜂數，雄蜂數與后蜂數各為37000隻，3900隻與3400隻。由於該聚落(colony)尚未進入生產繁殖個體的最終階段，因此還可能生產更多的雄蜂與后蜂。除了蜂巢結構、大小和生殖蜂的生產之外，本報告亦討論黑絨虎頭蜂特化的攻擊性與天敵之關係。

Key words:

**關鍵詞:** 社會性胡蜂、虎頭蜂、vespa basalis、蜂巢構造、台灣。

Full Text: PDF( 21.2 MB)

中華昆蟲 12: 1-11(1992)
Chinese J. Entomol. 12: 1-11(1992)

# A Huge Nest of *Vespa basalis* Collected in Taiwan (Hymenoptera: Vespidae)

**Sôichi Yamane** Biological Laboratory, Faculty of Education, Ibaraki University, Mito 310, Japan

## ABSTRACT

A mature nest of *Vespa basalis* Smith from Taiwan appears to be one of the largest hornet nests so far recorded. The nest was completely enveloped and had a moderately pointed roof cone and three vertical slit-like entrance holes on the side. It had 15 round combs with a total of 40,000 cells. The adults collected with the nest totaled 558 workers, 579 males and 535 new queens. The greater part of the adults, however, including most workers, escaped at the time of collection. The numbers of workers, males, and queens which the colony had produced (including cocooned stages) were estimated at 37,000, 3900, and 3400, respectively. The colony did not appear to be near the end of its productivity, so that it was likely to have produced many more males and queens. In addition to nest architecture, nest size and production of sexual forms, specialized aggressiveness of this species is discussed in relation to its natural enemies.

**Key words:** Social wasps, hornet, *Vespa basalis*, nest architecture, Taiwan.

# 採自台灣的黑絨虎頭蜂(*Vespa basalis*) (Hymenoptera: Vespidae)巨型蜂巢

**山根爽一** 茨城大學教育學部生物學研究室 **310** 日本國茨城縣水戸市文京 **2** 丁目

# 摘 要

在台灣中部埔里郊外採集的黑絨虎頭蜂成熟巢，可能是世界記錄最大的虎頭蜂巢。蜂巢卵形，大小(直徑×高)65×95公分，全體被外殼覆蓋，巢頂呈圓錐形。本蜂巢不見於其他種類的蜂巢構造特徵是外殼側面縱向的長形出入口。這巢共有三個出入口，形狀都是長形裂口(1×17公分)。蜂巢之內部有15個圓形巢脾，總計40,000多個蜂室。在巢內採集的成蟲數目包括558隻工蜂，579隻雄蜂與535隻后蜂。但在採取蜂巢時，成蟲幾乎全部為工蜂，有相當數目的成蟲逃逸了。估計羽化(含擬蛹與蛹)的工蜂數，雄蜂數與后蜂數，各為37,000隻，3900隻與3400隻。由於該聚落(colony)尚未進入生產繁殖個體的最終階段，因此還可能生產更多的雄蜂與后蜂。除了蜂巢結構、大小和生殖蜂的生產之外，本報告亦討論黑絨虎頭蜂特化的攻擊性與天敵之關係。


**關鍵詞**：社會性胡蜂，虎頭蜂，*Vespa basalis*，蜂巢構造，台灣。


## Introduction

Hornets (Genus *Vespa* of the Vespidae) are social wasps characterized by very large body size, moderately large colonies, and well advanced caste system (Akre, 1982; Matsuura, 1984). They have been the subject of comprehensive studies by Matsuura (1984) and Matsuura and Yamane (1990). Since the social system in wasps and bees is crudely related with the colony population size, it is interesting to know the maximum size of *Vespa* colonies, which can roughly be represented by the number of cells produced by the colony. Spradbery (1986) recorded a nest of *V. affinis picea* in New Guinea, which had 45,065 cells in twelve combs and seems to be the largest hornet nest so far recorded. According to other studies, the recorded largest numbers of cells per nest are about 14,000 for *V. simillima xanthoptera* Cameron in Japan (Matsuura and Yamane 1990) and *V. affinis* (Linnaeus) in the Philippines (Starr and Jacobson, 1990). There are suggestions that tropical and subtropical populations of these and some other species may build larger nests. *Vespa basalis* Smith is distributed in submontane and mountainous areas in South Asia, including Taiwan and India (Vecht, 1957), and has been inferred to construct the largest nests of its genus (Yamane, 1977; Kuo, 1985). However, its pugnacity and tendency to nest high in trees has discouraged detailed studies (Kuo, 1985). Many cases of nest collection have been reported in local newspapers and popular magazines in Taiwan, but without exact data.

I report here on a *V. basalis* nest collected in central Taiwan in October 1973, when the colony had attained maturity and begun producing new queens and males. This nest had a little more than 40,000 cells in 15 combs and seems to be the largest quantitatively recorded hornet nest in the world. Cell number is estimated as part of an overall description of the nest.

## Materials and Methods

### 1. Nesting site

*Vespa basalis* Smith is widely distributed in hilly and mountainous areas of Taiwan, and its nests were easily found until early in the 1980's. Since then, however, nest density has decreased with accelerated economic development and intensive collection of colonies for extermination and to produce "wasp liquor" (Kuo and Yeh, 1985, 1988). According to Kuo and Yeh (1985) the queens of *V. basalis* as well as those of *V. velutina* often found nests in subterranean cavities. *Basalis* queens may also supersedure *velutina* nests before worker emergence. During May and June colonies of the both species move to open places to build larger aerial nests. These secondary nests of *basalis* are mostly built on tree branches and bamboo stems at more than 10 m above the ground.

The nest was discovered in the summer of 1973 on a southeast-facing, steep slope covered with bushes and middle-sized trees at Tapingting (500 m), near Puli, Nantou County. It was hung from a branch of diameter 4.7 cm×5.9 cm of an unidentified broad-leaved tree. The nest site was about 4 m above the ground, somewhat lower than is usual for this species.

### 2. Collection

We collected the colony in the morning on 23 October 1973, using a protective clothing made of an ordinary rain wear, which gave effective protection with little loss in working flexibility. To gain access to the nest, we cut the tree. The strength and tenacity of the wasps' defensive response is of special note. We were forced to retreat more than once before we were able to bag the nest, and about 50 wasps pursued us as far as a point (Yamane, 1977: point R1 in Fig.4), a distance of nearly 100 m. It was necessary to close the road for a time and direct people onto a detour.

### 3. Measurements and estimation

The volume of the nest including outer envelope was estimated by summing the volumes of 158 horizontal sections derived from the reconstructed figure. The diameter of combs was measured with a plastic rule. That of cells (measured as distance between the opposite sides at the cell mouth) was measured with a caliper for 583 cells from 15 combs. The number of all small and large cells (for workers and queens, respectively) were counted on combs 1, 2, 14 and 15, whereas cell numbers on the other, larger combs were estimated from a count from half of each comb.

The number of adults was counted only for those left inside the nest. The eggs and exposed larvae were counted on 13 combs (all except for combs 10 and 11), and the cocooned brood on all combs. Except on combs 8 and 9, counts were done separately for small and large cells. Counts of "eggs" are in fact of egg-laden cells and are thus underestimated, as many cells had excess egg. The number of adults emerged was estimated in 500 cells from the number of meconia left in the cell bottom (after Yamane and Yamane, 1975). The number of emergences on each comb was calculated from this sample and the pattern of comb utilization. Given the healthy state of the colony, it is reasonable to assume that cocooned brood would have produced adult wasps and to incorporate them in the calculation. In order to estimate production of workers, queens and males separately, 332 small-cell and 197 large-cell pupae were sexed, from which the sex ratio [mlaes/(females+males)] was calculated for each comb. To know brood distribution patterns on the comb, utilization frequency of the same cell was determined. If cells of a given ring of uncocooned stages had no meconium, the ring was regarded as consisting of a first series of brood reared in those cells, and thus the uncocooned brood in cells with $n$ meconia represent the $(n+1)$th series of brood ($n$th series for cocooned and post deficated stages).

## Results

### 1. Nest architecture

(1) Gross architecture and size: As seen

in the presence of males and new queens, the colony was mature, so that the nest most probably had attained the final stage of its development. It was oval, and entirely enclosed in a thick envelope, and had a conical roof on the top and three vertical, slit-like entrances at the side (Figs. 1B, 2A, 2B). The maximum diameter and height were 65 cm and 95 cm, respectively, and the volume was estimated at 207 liters, of which 24 liters were taken up by the roof cone. The total area of comb-surface was 2.45 $m^2$ and the weight of the nest with brood probably exceeded 30 kg.

An immature nest, observed near Puli in late August 1972, had a round top and a circular entrance at the side (Fig. 1A).

(2) Envelope: As in other vespine nests, the envelope was made of woody fragments. It did not contain long fibers, such as are often used by the vespine subgenera *Paravespula* and *Vespula*. It was not laminate but for the most part it was imbricate, as in most aerial nests of other *Vespa* species. The imbrication was conspicuous on the lower half, less so on the upper half, and hardly evident on the roof, whose surface was plastered by daubing carton. The nest had a conical roof with an angle of 115° and more or less round at the tip. This roof was apparently built at a late stage, because the immature nest had no such roof cone. The height of the roof (from the underside of branch to the top) was 21 cm. Its outer wall was thick and the inside was filled with many pillars and plates, providing a cell-like structure of remarkable toughness. There were three vertical, slit-like entrances (Figs. 1B, 1B), facing east, southwest and west, respectively. One of these was measured at 1 cm wide and 17 cm long.

(3) Combs and cells: The nest consisted of 15 combs. As in some other species, these were round and flat with a slight elevation (dome) at the center (Fig. 2A). Some combs at the lower part, to which large cells had been lately added, bent upward peripherally. The uppermost comb (comb 1) was slightly oval, with dia-

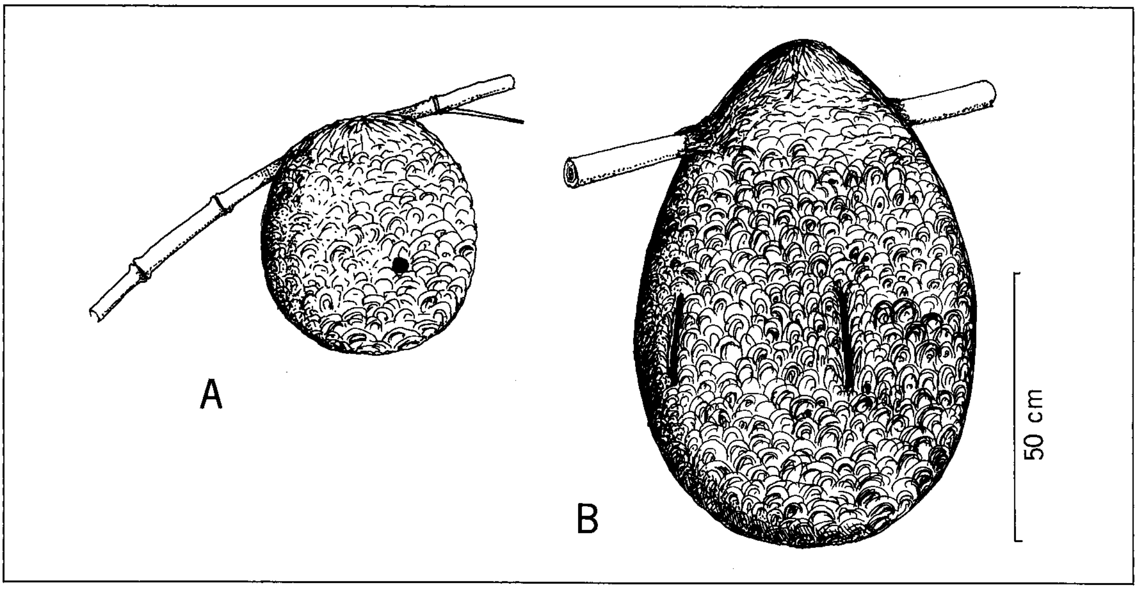


Fig.1 *V. basalis* nests at an early stage (late August at Yih-Chi, Nantou) (A) and a mature stage (late October, present nest) (B). Compare the roof top and entrance between the two nests.

meters of 12×13.5 cm, and the biggest one (comb 8) had a diameter of 57 cm. Each comb was attached to the one above by a thick central petiole and many thinner auxiliary petioles. Combs 2–4 and combs 10–15 were each suspended from the one above by fewer than 90 petioles, while each of the middle combs (6–9) had more than 100 petioles (Table 1). The number of side petioles connecting to the enve-


Fig.2 Mature nest of *V. basalis* with the inner structure exposed (A) and its slit-like entrance (B).

Table 1. Features of a mature *Vespa basalis* nest from central Taiwan. Combs are numbered sequentially from the top

| Comb No. | No. pillars to comb | No. pillars to envelope | No. small cells | No. large cells | Total cells |
|---|---|---|---|---|---|
| 1 | + | + | 261 | 0 | 261 |
| 2 | >11 | + | 933 | 0 | 933 |
| 3 | 61 | 11 | 1664 | 0 | 1664 |
| 4 | >74 | 35 | 2585 | 0 | 2585 |
| 5 | >122 | 15 | 3687 | 0 | 3687 |
| 6 | 121 | 5 | 4402 | 0 | 4402 |
| 7 | 121 | 2 | 4930 | 0 | 4930 |
| 8 | 106 | 5 | 4178 | 346 | 4524 |
| 9 | 113 | 4 | 2930 | 1220 | 4150 |
| 10 | 87 | 3 | 1647 | 2217 | 3864 |
| 11 | 75 | 5 | 367 | 2511 | 2878 |
| 12 | 52 | 2 | 0 | 2492 | 2492 |
| 13 | 34 | 0 | 0 | 1900 | 1900 |
| 14 | 23 | 0 | 0 | 1238 | 1238 |
| 15 | 11 | 0 | 0 | 578 | 578 |
| T | >1011 | >87 | 27584 | 12502 | 40086 |

+ : Present, not quantified.

lope was large in the upper combs, with a maximum of 35 in comb 4. The three lowest combs had no side petioles.

Cells were hexagonal and mostly in regular arrangement. However, on combs to which large queen cells were later added, there was a zone of irregular cells between the small and large cells. The cells clearly fell into two distinct size-types (Fig. 3). The average diameters for small cells (for workers and some males) and large cells (for queens and most males) were 7.1 mm (SE=0.3, $n$=300) and 9.4 mm (SE=0.6, $n$=203), respectively; these differed significantly ($t$-test, $p<0.001$). Their bottom sizes differed, too. Diameters of queen cells and male cells (9.8±0.3 mm and 9.6±0.3 mm, respectively, $n$=40 for each) from combs 12 and 13 also differed ($p<0.01$), while their bottom sizes did not differ. Small cells were larger at the periphery than at the center on each comb, and it increased as the stage advanced (6.7±0.3 mm for inner cells of comb 3 to 7.2±0.5 mm for comb 11, $p<0.05$; Fig. 3). Large cells were small at an earlier phase of nest growth (diameter, 8.5 mm, comb 8), then increased (max. 9.7 mm, comb 12) and again decreased (8.7 mm, comb 15). Cocoon cappings were white and round, protruding slightly beyond the cell mouth.

As seen in Table 1, the number of cells was about 260 in comb 1, attaining a peak of about 4900 in comb 7 and then gradually decreasing. The total number of cells was estimated at 40,100 (27,600 small cells and 12,500 large cells). Combs 1–7 had only small cells and combs 12–15 only had large cells, with the proportion of large cells increasing through combs 8–11.

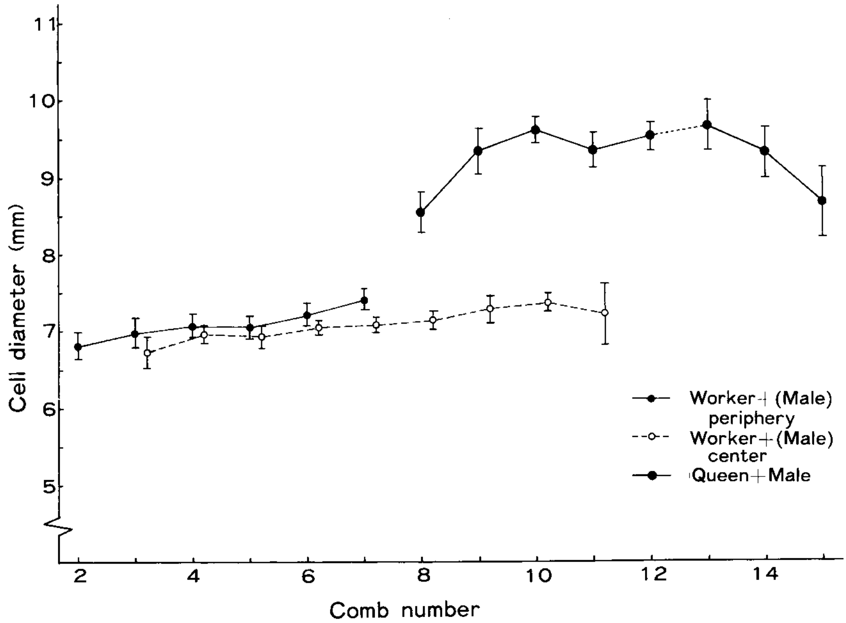


Fig.3 Changes in cell diameter (side to side) in relation to construction sequence of combs. Those of small cells and large cells are separately shown. Vertical lines indicate standard errors. Values of queen- and male-cells for combs 8-12 are based on peripheral cells, while those for combs 13-15 are based on cells from throughout the comb.

## 2. Adult and brood compositions

558 workers, 579 males and 535 new queens were collected inside the nest. The greater part of the adults, most of which were almost certainly workers, escaped at the time of collection. I roughly estimate the total number of workers present at more than 5000.

Table 2 shows the composition of immature populations on 15 combs. The number of small-cell eggs was about 10,000 on combs 2–7, while that of large-cell eggs on combs 12–15 was 2300. Comb 1 had no eggs, and comb 6 had the largest number of eggs (3349) among the combs counted. If combs 8–11 had been censused for eggs, the total number would likely reach 18,000–19,000. Most large cells at the periphery of combs 12–14 had two or three excess eggs. Larvae were few in small cells (90 larvae in combs 6, 7), while abundant in large cells (1317 in combs 12–15). The total number of larvae (excluding combs 10 and 11) was about 2100. The numbers of small and large cells with cocoon were about 2600 and 4200, respectively.

## 3. Number of adults produced

The number of cells which produced at least one adult (including cocooned brood) was about 30,000 or 76.8% of all cells. Fewer than half of these produced more than one audlt (Table 3). The maximum number of emergences per cell was four on combs 1–3, three on combs 4–9, two on comb 10, and one on combs 11–14. Comb 15 had no sign of emergence. The numbers of workers, males and new queens produced were estimated at 37,600, 4000 and 3400, respectively (Table 3). Judging from the remaining worker force and immature composition of the colony, many more males and queens could have been produced if the colony had run its normal course.

The sex ratio in samll cells steadily increased in lower combs (0.01 on comb 6 to 0.60 on comb 10) with an average of 0.17. In contrast, the ratio in large cells varied irregularly between 0.16 and 0.65 with an average of 0.45.

## 4. Pattern of comb and cell utilization

Combs are, as a rule, separately used for rearing workers and queens (Fig. 4A). The upper seven combs had only small cells (18,500 in total, Table 1), of which combs 1–5 produced workers alone and combs 6–7 produced workers and a few males. Four middle combs (combs 8–11) had 9100 samll cells centrally and 6300 large cells peripherally, with increasing proportions of large cells in lower combs. The remaining combs (combs 12–15) consisted entirely of 6200 large cells. Judging from the brood distribution (Fig. 4B), large cells were initiated first on comb 11, surrounding a central area of small cells that was 170 mm in diameter. Then, comb 12 of large cells was initiated and large cells were added to the periphery of three upper combs (combs 8–10). The innermost large cells of comb 11 and central cells of comb 12 had already produced adults and contained a second series of eggs. This suggests that the production of sexual forms in this colony commenced in early September (about 40 days before the collection).

# Discussion

## 1. Specialized aggressiveness and natural enemy

The alert response of *V. basalis* workers to human beings is distinctively active even at first contact. They often attacked during their usual alert flight when we approached within about 30 m of the nest. When an alerting wasp of *V. basalis* locates a new object, she usually flies around suspiciously and then attacks the object if it moves. Alternatively she will sometimes alight on the object with no sign of agitation and suddenly sting it. It is for this reason, that among Taiwanese *Vespa* species, *V. basalis* is most feared by people, especially those working in forest and agriculture. Other species,

Table 2. Immature populations on 15 combs, estimated for small cells and large cells separately

| Comb No. | Small cells | | | | Total No. in small cells | Large cells | | | | Total No. in large cells | Small + Large cells | | | | | Total No. immat. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | eggs | larvae | cocoons | | | eggs | larvae | cocoons | | | eggs | larvae | cocoons | | | |
| | | | worker | male | | | | queen | male | | | | worker | queen | male | |
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 2 |
| 3 | 168 | 0 | 0 | 0 | 168 | 0 | 0 | 0 | 0 | 0 | 168 | 0 | 0 | 0 | 0 | 168 |
| 4 | 1125 | 0 | 0 | 0 | 1125 | 0 | 0 | 0 | 0 | 0 | 1125 | 0 | 0 | 0 | 0 | 1125 |
| 5 | 2658 | 4 | 0 | 0 | 2662 | 0 | 0 | 0 | 0 | 0 | 2658 | 4 | 0 | 0 | 0 | 2662 |
| 6 | 3349 | 24 | 115 | 1 | 3489 | 0 | 0 | 0 | 0 | 0 | 3349 | 24 | 115 | 0 | 1 | 3489 |
| 7 | 2755 | 66 | 608 | 12 | 3441 | 0 | 0 | 0 | 0 | 0 | 2755 | 66 | 608 | 0 | 12 | 3441 |
| 8 | + | + | 543 | 88 | ? | ? | ? | 1 | 0 | ? | 2368 | 151 | 543 | 1 | 88 | 3151 |
| 9 | + | + | 342 | 324 | ? | ? | ? | 150 | 62 | ? | 1503 | 541 | 342 | 150 | 386 | 2922 |
| 10 | + | + | 240 | 352 | ? | ? | ? | 207 | 255 | ? | ? | ? | 240 | 207 | 607 | ? |
| 11 | + | + | 0 | 0 | ? | + | + | 348 | 647 | ? | ? | ? | 0 | 348 | 647 | ? |
| 12 | 0 | 0 | 0 | 0 | 0 | 770 | 330 | 652 | 735 | 2487 | 770 | 330 | 0 | 652 | 735 | 2487 |
| 13 | 0 | 0 | 0 | 0 | 0 | 560 | 563 | 656 | 121 | 1900 | 560 | 563 | 0 | 656 | 121 | 1900 |
| 14 | 0 | 0 | 0 | 0 | 0 | 457 | 370 | 173 | 143 | 1143 | 457 | 370 | 0 | 173 | 143 | 1143 |
| 15 | 0 | 0 | 0 | 0 | 0 | 470 | 54 | 0 | 0 | 524 | 470 | 54 | 0 | 0 | 0 | 524 |
| T | 10057 | >94 | 1848 | 777 | >12776 | >2257 | >1317 | 1963 | 2187 | >7724 | >16185 | >2103 | 1848 | 2187 | 2740 | >25063 |

+ : Present, not quantified.
? : Unknown.

Table 3. Frequency distribution of numbers of workers, queens and males produced in cells

| Comb No. | No.cells (small + large) produced adult[1) once | twice | 3 times | 4 times | total | No. adults produced[1) worker | queens | males | Total No. adults produced |
|---|---|---|---|---|---|---|---|---|---|
| 1 | 60 | 151 | 36 | 4 | 251 | 486 | 0 | 0 | 486 |
| 2 | 277 | 358 | 179 | 23 | 837 | 1622 | 0 | 0 | 1622 |
| 3 | 532 | 780 | 170 | 7 | 1489 | 2630 | 0 | 0 | 2630 |
| 4 | 872 | 915 | 180 | 0 | 1967 | 3242 | 0 | 0 | 3242 |
| 5 | 1554 | 1076 | 410 | 0 | 3040 | 4936 | 0 | 0 | 4936 |
| 6 | 1999 | 1685 | 219 | 0 | 3903 | 6023 | 0 | 3 | 6026 |
| 7 | 2145 | 2150 | 64 | 0 | 4359 | 6625 | 0 | 12 | 6637 |
| 8 | 1638 | 2170 | 59 | 0 | 3867 | 5994 | 79 | 82 | 6155 |
| 9 | 1952 | 1562 | 4 | 0 | 3518 | 3973 | 561 | 554 | 5088 |
| 10 | 2451 | 601 | 0 | 0 | 3052 | 1799 | 673 | 1181 | 3653 |
| 11 | 1992 | 0 | 0 | 0 | 1992 | 289 | 596 | 1107 | 1992 |
| 12 | 1437 | 0 | 0 | 0 | 1437 | 0 | 676 | 761 | 1437 |
| 13 | 777 | 0 | 0 | 0 | 777 | 0 | 656 | 121 | 777 |
| 14 | 316 | 0 | 0 | 0 | 316 | 0 | 173 | 143 | 316 |
| 15 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| T. | 18002 | 11448 | 1321 | 34 | 30805 | 37619 | 3964 | 3414 | 44997 |

[1) Estimates involve cocooned stages.

except *V. mandarinia*, only attack human beings within narrower ranges (1–10 m) from their nests. They usually escape when disturbed at remote places from

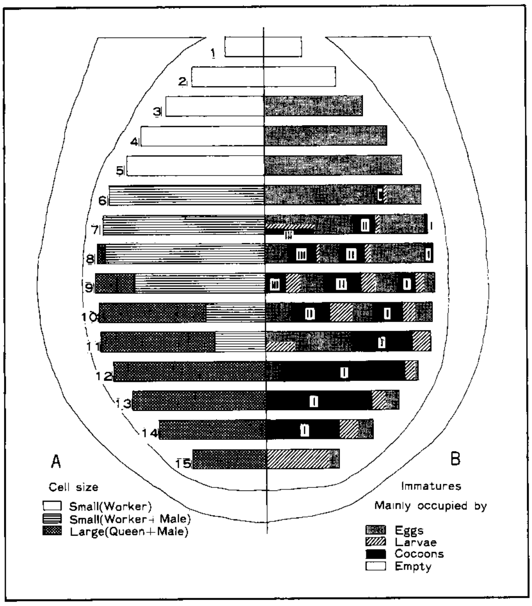


Fig.4 Distribution pattern of small and large cells (A) and that of immature stages on different combs (B). Roman numerals I-III indicate the first to third series of cocooned stages reared in the same cells, respectively.

their own nests. The response of *basalis* workers to disturbance at the nest is also distinct. Even a slight mechanical stimulus can cause great numbers of wasps to rush from the nest at once. The presence of a large worker population and multiple slit-like entrances allows for such a rapid on-guard reaction.

Why has such a special aggressiveness arisen in this species or at least in the Taiwan population ? No actual predation of *V. basalis* colonies by natural enemies have been observed. The extremely wide alert range and rapid defensive mobilization suggest an adaptation to large, visually hunting animals, such as Taiwanese black bear (*Selenarctos tibetanus formosanus*) and Taiwanese macaque (*Macaca cyclopis*). These omnivorous mammals are known to eat broods of social wasps and bees. They climb well and could cause serious damage to nests built even on small branches.

An example of possible attack on *V. basalis* by a macaque was observed near Puli by a local person. On an October morning more than 50 years ago, the late Mr. Shun-Sheng Chong reached a point from which he had a good view of a big *V. basalis* nest at a distance of about 150 m. The nest was hung from the branch of Chinese cork oak tree (*Quercus variabilis*) at a height of about 15 m. A troop of approximately 100 monkeys was on the ground around the tree. Usually these monkeys came to the cork oak trees in Autumn for their fruits. A big monkey, probably a male adult, was climbing up the tree. Although many wasps rushed out at him, he reached the nest, covered his face with a hand, and broke the envelope to expose combs. Striking the nest repeatedly, so that some fragments fell to the ground, the monkey descended to the ground, and many others came to the point where the fragments lay. They appeared excited. Mr. Chong could not tell if the climing monkey or any others were stung, nor did he confirm that they ate the fallen combs, but the event strongly suggests predation by individuals with some experience with tree-nesting hornets as prey.

Some rodents are also known to climb trees, but they do not seem to give serious damage to the wasp colonies. The honey buzzard (*Pernis ptilorhynchus*) is a predator on wasp and bee colonies in Taiwan (Prof. K.Y. Lue, pers. com.), but it is assumed to attack only vulnerable colonies at early developmental stages. Prof. M.C. Kuo (pers. com.) once observed an eagle attacking a large *V. basalis* nest. To clarify the evolution of aggressive behavior in this species, habits and impacts on wasp colonies of tree climbing mammals and predatious birds should be studied in various districts.

**2. Architecture of nest**

The nest structure of *V. basalis* resembles that of other arboreal species of Vespinae, in that the nest consists of a series of horizontal, round combs with a thick envelope surrounding them (Yamane, 1977; Matsuura, 1984; Starr and Jacobson, 1990). However, the roof area of arboreal nests varies according to climatic conditions. In temperate districts (with annual precipitation<2000 mm) roofs are round and virtually devoid of a conical helmet (Yamane, 1977; Matsuura, 1984). In contrast, those in the humid tropics of Southeast Asia, e.g., Sumatra and the Malay Peninsula (annual precipitation 2000–5000 mm), except that of *V. luctuosa*, have a sharply pointed top, which is built up as the nest develops (Starr and Jacobson, 1990). Nests in Taiwan (annual precipitation mostly 2000–3000 mm) have a moderately pointed roof. Thus the roof top become sharper in parallel with the increase of annual rain fall and the occurrence of squalls that are often seriously destructive.

Vertical slit–like entrances are so far unique to *V. basalis* (Yamane, 1977). The entrance is round at earlier stages and later elongates, while very large nests add one or more entrances (Kuo and Yeh, 1985; this paper). Nests of other species have a smaller round entrance (Matsuura, 1984; Starr and Jacobson, 1990) which does not allow wasps to rush out *en masse*. Starr and Jacobson (1990) stated that the entrance hole is round in early nests of *V. affinis* in the Philippines, but elongated somewhat into a vertical oval in many mature nests, often twice as long as wide. However, this does not approach the slit–like condition seen in *V. basalis*. *V. velutina*, which also constructs huge nests, often makes round, protruding entrances (Kuo and Yeh, 1985).

**3. Nest size**

Spradbery (1986) recorded a huge nest of *V. affinis picea* in New Guinea. It had 45,000 cells in twelve combs and seems to be the largest hornet nest on record to date. Starr and Jacobson (1990) summarized the known features of mature nests of *Vespa* species. The largest nests listed there were of *V. affinis* in the Philippines (Starr and Jacobson, 1990) and *V. simillima xanthoptera* in Japan (Matsuura, 1984), each with an estimated 14,000 cells. One of the largest *affinis* nest in the Philippines consisted of nine combs with a total of 12,000 cells, a comb–surface area of about 0.8 $m^2$ and an estimated volume of 140 liters (Starr and Jacobson, 1990). Kuo and Yeh (1985) recorded some parameters of eight *V. basalis* nests collected in Taiwan between March and the following February. Their data are not strictly comparable with mine, but the biggest nest (collected in December) had 16 combs and about 18,000 adult and 2000 immature wasps. Its outer diameter and height were 65 cm and 87 cm, respectively, so that it was of comparable size to the present nest. According to Prof. Kuo's personal communication, a villager in Nan–Liuo found in November 1981 a huge nest of this species with a height of 200 cm and a diameter of 150 cm, and possibly with more than 50,000 cells. Since *V. basalis* mostly constructs huge nests as large as the present one, it may be regarded as the hornet species that constructs the largest nests among hornets.

Nest size is not easily compared among different vespid taxa, because it can be represented by different parameters, such as volume, comb–surface area, number of cells, and adult population. The species so far known to build the biggest nest among the Vespinae is *Vespula germanica* introduced into Australia and New Zealand. Nests of this species can weigh up to 450kg with 4 million cells and up to 300,000 adults (Spradbery, 1973). A neotropical polistine wasp, *Agelaia vicina*, has been reported to construct a nest with a comb–surface area of 33 $m^2$ and up to 1.3 million adult wasps (Jeanne, 1991). A common feature of these species is that their colony cycles are long and often perennial.

Hornet nests are much smaller both

in terms of maximum volume and maximum population than those of the above mentioned species. This may be related to the length of the colony cycle, which is annual even in the tropics. It is an open question why *Vespa* colonies are not perennial, in even relatively non-seasonal environments.

**4. Production of sexual forms**

The pattern of sexual production in the studied colony is similar to that seen in most other vespines (Spradbery, 1973, Matsuura, 1984). The sexual forms are produced in the latter part of the colony cycle. Queens are reared only in large cells, and males in (mainly) large and small cells. Queen and male eggs were not laid separately in discrete areas, but apparently randomly among large cells. Worker production was continued in parallel with sexual production, consistent with Greene's (1984) findings.

## Acknowledgments

I thank Mr. A. J. Wang, Mr. J. C. Wang, Mr. C. S. Lin, Mr. C. Wu for help at the nest collection, the late Mr. S. S. Chong for valuable information about vespine biology and possible predation on *V. basalis* nest by Taiwanese macaque monkeys, Prof. K. Y. Lue for suggestions on possible vertebrate predators at hornet nests, and Dr. C. K. Starr, Prof. M. Matsuura and Prof. M. C. Kuo for critical comments on the manuscript.

## References

**Akre, R. D.** 1982. Social wasps. pp.1–105 *in* H.R. Hermann, ed. Social insects, Volume IV. Academic Press, N.Y.

**Greene, A.** 1984. Production schedule of vespine wasps: an empirical test on bang-bang optimization model. J. Kansas Entomol. Soc. 57: 545–568.

**Jeanne, R. L.** 1991. Social biology of the swarm-founding Polistinae. pp.191–231 *in* K.G. Ross and R.W. Matthews, eds. Social biology of the vespid wasps. Cornell University Press. Ithaca, N.Y.

**Kuo, M. C., and W. H. Yeh.** 1985. Ecological studies on *Vespa basalis* Smith, *Vespa velutina flavitarsus* Sonan and *Vespa tropica pseudosoror* Vecht (Study on Vespidae in Taiwan II). J. Nat. Chiayi Inst. Agr. 11: 95–106.

**Kuo, M. C., and W. H. Yeh.** 1988. Study on the effects of wasps on the homeostasis of forest population in Taiwan. J. Nat. Chiayi Inst. Agr. 17: 79–97.

**Matsuura, M.** 1984. Comparative biology of the five Japanese species of the genus *Vespa* (Hymenoptera, Vespidae). Bull. Fac. Agr. Mie Univ. 69: 1–131.

**Matsuura, M., and Sk. Yamane.** 1990. Biology of the vespine wasps. Springer-Verlag, Berlin, 322 pp.

**Spradbery, J. P.** 1973. Wasps. An account of the biology and natural history of social and solitary wasps. Sidgwick and Jackson, London, 408 pp.

**Starr, C. K., and R. S. Jacobson.** 1990. Nest structure in Philippine hornets (Hymenoptera, Vespidae, *Vespa* spp.). Jpn. J. Entomol. 58: 125–143.

**Vecht, J. van der.** 1957. The Vespinae of the Indo-Malayan and Papuan areas (Hymenoptera, Vespidae). Zool. Verh. 34: 1–83.

**Yamane, S.** 1977. On the collecting technique of vespine nests, based chiefly on practices through a survey in Taiwan from 1972 to 1974 (Hymenoptera, Vespidae). Seibutsu Kyozai (Kikonai, Hokkaido) 12: 42–59 (in Japanese).

**Yamane, S., and Sk. Yamane.** 1975. Investigating methods of dead vespine nests (Hymenoptera, Vespidae). Seibutsu Kyozai (Kikonai, Hokkaido) 10: 18–39 (in Japanese).

***Received for publication December 18, 1991; revised manuscript accepted Febrnary 7, 1992.***