

# Comparative biology of the five Japanese species of the genus *Vespa* (Hymenoptera, Vespidae)

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## INTRODUCTION

The subfamily Vespinae is distributed mainly in the northern hemisphere, particularly in the temperate zones. This subfamily contains only four genera, *Provespa*, *Vespula*, *Dolichovespula* and *Vespa*. Leaving *Provespa*, a small genus which is represented by three species found only in Southeast Asia, the other three were prosperous genera developed different modes of life, though with a considerable overlap. Neither *Vespula* nor *Dolichovespula* is distributed in tropical regions, and they are completely adapted to temperate climates. The genus *Vespa* is mostly distributed in the Indo-Malayan area, but some of the species are found to be dominant in temperate regions.

According to EDWARDS (1980) the genus *Vespa* has 22 species and of these, seven species are distributed as far north as Japan (MATSUURA and YAMANE 1984). In temperate Europe, there is only one species, *Vespa crabro*, which has also dispersed secondarily to North America, where no endemic species occurred. In contrast to *Vespula* and *Dolichovespula*, the bionomics of *Vespa* have so far been less well studied both in Europe and North America, probably because of the small number of species and their highly aggressive disposition, despite of the pioneer works of JANET (1903) in France. While the greatest strides in our understanding of hornet biology have been undertaken on the oriental hornet, *Vespa orientalis* in Israel since BODENHEIMER (1930, 1933), ISHAY (1964 - ) and his colleagues have now made intensive studies on the ethology and physiology of this species.

In Japan, which seems to have most representatives of this genus in the temperate regions, many of the reports on the life of the hornets are only general descriptions and very few give detailed data.

Since 1957 I have been engaged in biosociological studies on this group and have obtained some information on the bionomic and ethological characters of this genus in Japan. The present study intends to approach the comparative socio-biology of Japanese *Vespa* hornets through extensive ecological research of their habits and life history. It is hoped that this article will provide a basis for future comparative studies not only within the genus, but also for comparison with other social wasps.

## METHODS

### Study area

The field work in the present paper was mainly carried out in and near Kibi-cho, Wakayama Pref., southern Japan (Fig. 1). Kibi is a small town along the River Arita, situated ca. 20km south of Wakayama City, about



Fig. 1. The map of the Japan and the study area.

Table 1. Main climatic conditions in Kibi (1962 - 1975)

Month	Temperature ( $^{\circ}\text{C}$ )			Rainfall (mm)
	Mean maximum	Mean	Mean minimum	
Jan	9.1	4.8	0.7	81.7
Feb	9.5	5.3	0.9	68.3
Mar	13.0	8.1	3.1	119.7
Apr	19.3	14.5	9.7	187.7
May	23.5	18.5	13.5	168.3
Jun	26.0	21.9	17.6	238.9
Jul	30.3	26.3	22.2	231.6
Aug	31.4	27.0	22.7	209.7
Sep	27.7	23.4	19.0	209.9
Oct	21.8	17.4	12.7	133.6
Nov	16.9	12.2	7.3	92.2
Dec	12.2	7.7	3.5	66.4
Mean	20.0	15.5	11.0	Total 1825.0
Extremes	35.7		-5.4	

50~250m above sea level. Main climatic conditions in the locality are given in Table 1. The average climatic conditions are: mean air temperature  $15.5^{\circ}\text{C}$ , the hottest month August (mean  $27.0^{\circ}\text{C}$ , mean maximum  $31.4^{\circ}\text{C}$ ) and the coldest month January (mean  $4.8^{\circ}\text{C}$ , mean minimum  $0.7^{\circ}\text{C}$ ), mean annual rainfall 1825.0mm, being most abundant in June (238.9mm) and July (231.6mm). Until recently the area had been covered with secondary mixed forests mainly consisting of pines, deciduous oaks, cherries, etc., with some remnants of the primary lucidophyllous forest, *Shilia*, *Camelia*, etc. In recent years the forests are rapidly diminishing, replaced by rural or suburban areas.

The area is remarkable in its abundance of *Vespa* colonies, and five species, namely *V. mandarinia japonica*, *V. analis insularis*, *V. crabro flavofasciata*, *V. simillima xanthoptera* and *V. tropica pulchra*, are found throughout their active season. The following descriptions are given mainly based upon these five species.

### Methods of Observations

The data for this study were gathered mainly in the field in and near Kibi-cho during the period from 1964 to 1975. During the course of this study extensive observations in the field have been made, more or less continuously, on annual life cycles, nesting habits, food habits, and activities of adults inside and outside the nest.

*Nesting habits:* Many nests were located by extensive search in the study area, or by following queens and/or workers flying from bait stations or food sources to the nesting site. Some locations of nests were reported by local residents.

All the nests were numbered according to the order of finding of each species every year. A total of 622 nests were observed in and near the study area over the past twelve years, and consisted of 288 nests of *V. simillima*, 164 of *V. analis*, 80 of *V. crabro*, 56 of *V. mandarinia*, and 34 of *V. tropica*.

*Food habits:* Observations on food habits were made not only in the field but also at the nest entrance, where returning foragers with prey were collected to examine the species of prey. Data on phenology of hornets captured by traps attached to hives were prepared not only from the samples in Kibi, but from those offered by several bee keepers in Akita, Yamaguchi, Fukuoka and Nagasaki Prefectures.

The field work on the behaviour of intra- and interspecific dominance relationships among post-hibernation queens at food sources was carried out at different groves of *Quercus* trees during the period from April to late July both in 1966 and 1967. In 1966 the observations were made at a grove consisting of 7 *Quercus acutissima* and 3 *Q. glauca*, which were 7–10m in height, of which 2 trees secreted tree sap. In 1967 the observations were made at a hilly elevation 244m high, where the vegetation was a copse consisting of 10 *Q. acutissima*. In order to distinguish each individual, in both years all the queens of *Vespa* that visited the tree aperture were marked with colour oil-paints on their mesonotum, according to the order of finding of each species when she had alighted on the trunk near by the tree aperture. Observations were made at as near a place as possible and in the evening an electric torch was used to light the hornets.

*Qualitative and quantitative changes of queen activities:* The study was carried out mainly on an incipient nest of *V. crabro* (C6601) attached to the ceiling of the attic of a storehouse in Shimotsu-cho, Wakayama Pref. in 1966. The nest was situated about 50cm from the window and individuals of the nest had to take a route on foot 37cm along the wall and 50cm along the ceiling to reach the nest. Observations were made for 28 days (120 hours) during the period from June 2nd to July 28th in 1966 at irregular intervals. At the last observation on July 27th, the nest consisted of two combs and 190 cells with a queen and 15 workers, which were killed by insecticide sprayed around the nest on July 28th.

*Relations between labour and day age in workers:* The study was carried out with queen-right colonies of five species, *V. simillima*, *V. analis*, *V. crabro*, *V. mandarinia* and *V. tropica*. Newly emerged workers in each species were given an individual mark on their thorax with oil-paints on the day of emergence. In four species, *V. tropica*, *V. analis*, *V. crabro* and *V. mandarinia*, newly emerged workers on the combs were carefully marked without picking them up from the comb surface. In *V. simillima* it is very difficult to mark the thorax directly of newly emerged workers on the combs without any disturbance because they quickly irritated. Therefore, I took workers within about 10 hours after emergence from another colony (S6802) of the same species which was kept in another nest box, and released them into the observation nest after marking. These teneral workers were always accepted within one day without any signs of hostility, and they immediately joined the indigenous workers in performing any tasks in the nest.

The total number of individually marked workers was 57 in *V. simillima*, 35 in *V. analis*, 39 in *V. mandarinia*, 36 in *V. tropica* and 80 in *V. crabro*, respectively, and all of them were followed to estimate not only the day of the first foraging but also the longevity of workers. Of these marked workers, all the activities were observed on some individuals during their adult life at irregular intervals in the daytime and recorded together with the duration spent in each activity within the error of about  $\pm 3$  seconds. The nests observed are presented in the following notes(p.5).

*Division of labour in orphan colonies:* Observations on orphan colonies were mainly made on a nest of *V. analis* (A6705), which was collected in Nachikatsuura-cho, Wakayama Pref. on July 23rd, 1967. The colony



Species	<i>simillima</i>	<i>analis</i>	<i>mandarina</i>	<i>tropica</i>	<i>crabro</i>
Nest observed	S6801	A7207	M7401	T6803	C6601
No. of workers observed	3	2	2	2	4
Individual No.	Nos.8,9,10	Nos.3,4	Nos.5,6	Nos.2,3	Nos.38,39,40,41
Time of emergence	12:00 – 16:00 July 12th 1986	12:10, 12:50 August 3rd 1972	8:20, 12:20 July 28th 1974	12:00 – 15:00 July 25th 1968	8:30 – 16:00 July 21st 1966
Total time of observation	25 days (102h)	28 days (82h)	27 days (81h)	60 days (140h)	28 days (70h)

with all nest members (1 queen and 16 workers) was introduced into an observation box which was connected with the exterior by means of a bamboo tube. The queen was removed artificially on the day of collecting and returned to the original nest the second day after removal. But she was immediately attacked and killed by the workers. All the workers at time of collecting the nest were marked with colour oil-paints on their mesonotum. A total of 72 hours (50 days) of observation was made on the behaviour of the 10 marked workers during the period from July 23rd to September 15th.

*Survivorship of colony members:* In preparing life tables survival data for brood and adults of five *Vespa* species, i.e., *simillima*, *analis*, *mandarina*, *tropica* and *crabro*, were obtained from different sources, and combined into one due to some technical difficulties in following the whole life history of particular individuals from egg to adult stage.

Observations in each species were made principally on the colonies listed earlier. But, in *V. tropica* the data from a nest (T7401), which I observed during the entire period from nest foundation to disintegration are used. In order to determine the length of each developmental stage and its survival in successive immature stages they were divided into three stages; eggs, larvae in each instar and cocoons. Each brood cell was daily mapped and photographed throughout the observation periods. Cell maps were made once a day, and the dates of oviposition, hatching, cocoon spinning and emergence of individuals of the brood were estimated from them. These events were regarded to have occurred on the day when first recorded. The survival of brood during the cocoon period could not be observed directly because of its technical difficulty, and larvae or pupae within cocoon cell were regarded as alive when the cell caps remained normal. The death of brood was also ascertained by the empty cells in brood circles, because the brood in a comb exist in concentric circles of eggs, larvae and cocoons, and blanks in brood rings indicate where death has occurred (SPRADBERY 1973).

All the newly emerged workers were not observed directly at the time of emergence and successful emergence was confirmed by the existence of teneral workers which usually inserted their body into the empty cell from which they had just emerged. In order to estimate the longevity of workers, newly emerged workers were given an individual mark on the mesonotum with paints on the day of emergence. The total number of individually marked workers in each species has already been mentioned. Each individual was checked from day to day and the examination was made principally every evening after their flying activity had ceased, with occasional inspection in the daytime, until the disappearance of all marked workers in each colony. The worker's last day alive was assumed from the date when each individual did not return to the nest any more, because workers almost never died in the nest.

*Seasonal change in population structure:* In order to estimate the seasonal changes in the population structure of each species I collected a total of 393 nests in all stages of development from 1964 to 1975, which consisted of 150 nests of *V. simillima xanthoptera*, 122 nests of *V. analis insularis*, 38 nests of *V. crabro*

flavofasciata, 49 nests of *V. mandarinia japonica* and 34 nests of *V. tropica pulchra*. All of the nests except large colonies of *V. simillima* were taken with returning workers, which were captured when the nest was revisited about one or two hours later in the daytime. A number of *V. simillima* nests at the later stage of nesting were occasionally taken in the evening with the help of chloroform and all anesthetized workers inside or on the envelope were collected to examine the complete contents. The number of combs, cells, pillars, immature stages and adults were counted in each nest on the day of collecting.

Development of a single colony was also observed on a nest of *V. tropica* (T7401) which was founded in a wooden box at Wakayama Fruit Tree Experimental Station in Kibi on June 9th, 1974. Changes in the colony development and population structure of the nest were followed at its natural site during the active period from nest foundation to disintegration on October 15th, 1974.

*Nest survival*: During the observation period I found a total of 59 nests of *V. analis insularis* at an incipient stage. These nests were censused at irregular intervals in the field until the end of each nest. The data from many unsuccessful nests of each species found in the field, together with my successive observations on the active nests, gave some information to estimate the survival of *Vespa* colonies and various factors contributing to colony termination.

*Annual fluctuation of colony numbers*: The records are mainly based upon the mature nests of the five species, *V. simillima*, *V. analis*, *V. crabro*, *V. mandarinia* and *V. tropica*, which have been observed in and near the survey area during a 12-year period from 1964 to 1975. Besides, a systematic search for all colonies of *V. simillima* in the study area was made annually in late autumn, when the colonies had almost completed their nests, during the period from 1964 to 1975. The area, covering 300 hectares consists of four sub-areas, Mutugawa in Kanaya-cho (ca. 75 ha), Yoshikawa in Kanaya-cho (ca. 80 ha), Yoshimi in Kibi-cho (ca. 50 ha), and Yamada in Yuasa-cho (ca. 95 ha), all of which are villages among the hills of about 50-500 meters in height.

## TAXONOMY AND DISTRIBUTION

The superfamily Vespoidea is divided into three families; Masaridae, Eumenidae and Vespidae (RICHARDS 1962, 1972). The social wasps or Vespidae fall into three subfamilies; Stenogastrinae, Polistinae and Vespinae. According to his most recent revision of the Vespinae, EDWARDS (1980) recognized four generic names: *Provespa* Ashmead, *Vespula* Thomson, *Dolichovespula* Rohwer and *Vespa* Linnaeus. The vespine genera are primarily a tropical Asian group and have penetrated into the temperate regions of Eurasia and North America. All vespines are eusocial or social parasites on their eusocial relatives and are noteworthy for the advanced state of sociality relative to most of the Polistinae.

The genus *Vespa* is distinguished from other Vespinae primarily by its large size and the expanded condition of the rear part of the head (BEQUAERT 1930, 1931, DUNCAN 1939, VECHT 1936, 1957). The original description of *Vespa* made by LINNAEUS (1758, Systema Nature) comprised all the then known species now included in the subfamily. The genus *Vespa* has been revised by SAUSSURE (1853-1858), THOMSON (1869), BUYSSON (1903-1905), BEQUAERT (1930-1939) and VECHT (1959), and as presently delineated it contains approximately 22 species which are mainly centered in southeastern Asia. Only two species, *V. crabro* and *V. orientalis*, are widely distributed in the western half of the Palaearctic region.

In Japan the following forms have so far been recorded (MATSUURA and YAMANE 1984):

Forms	(Japanese name)
1. <i>V. affinis affinis</i> LINNAEUS 1764 Distribution. Ryukyu islands.	(Tsumaguro-suzumebachi)
2. <i>V. analis insularis</i> DALLA TORRE 1894 Distribution. The whole country.	(Kogata-suzumebachi)
3. <i>V. crabro flavofasciata</i> CAMERON 1903 Distribution. The whole country.	(Mon-suzumebachi)
4. <i>V. dybowskii</i> ANDRE 1884	(Chairo-suzumebachi)

- Distribution. Hokkaido, Honshu (Central).  
 5. *V. mandarinia japonica* RADOSZKOWSKI 1857 (Ô-suzumebachi)  
 Distribution. The whole country.  
 6. *V. simillima simillima* SMITH 1968 (Kebuka-suzumebachi)  
 Distribution. Hokkaido.  
 7. *V. simillima xanthoptera* CAMERON 1903 (Kilro-suzumebachi)  
 Distribution. Honshu, Shikoku, Kyushu.  
 8. *V. tropica esakii* SONAN 1935 (Esaki-suzumebachi)  
 Distribution. Tsushima island.  
 9. *V. tropica loochooensis* BEQUAERT 1936 (Okinawahime-suzumebachi)  
 Distribution. Ryukyu islands.  
 10. *V. tropica pulchra* BUYSSON 1905 (Hime-suzumebachi)  
 Distribution. Honshu, Shikoku, Kyushu.

Also two forms, *V. bicolor* FABRICIUS 1787 and *V. walkeri* BUYSSON 1905, are recorded from Japan. The former species recorded by BUYSSON (VECHT 1957) in all probability does not occur in Japan and the latter recorded from Central Japan by VECHT (1959) is unknown to me as I have thus far not encountered the form coinciding with the original description (BUYSSON 1905).

### I. ANNUAL CYCLE

In temperate regions *Vespa* colonies are annual and the new colonies are always begun in the spring by a single fecundated queen. The annual life cycle of *Vespa* as presented subsequently in this chapter consists of the following six periods (Fig. 2), though a little variation in details of the cycle occurs among the species: 1) Pre-nesting, 2) Solitary, 3) Cooperative, 4) Polyethic, 5) Reproductive, 6) Hibernating. The sequence does not essentially differ from that in other temperate eusocial insects with annual colonies; *Vespula*, *Bombus* and, with some deviations, *Polistes* and eusocial halictine bees. A brief resume is given here.

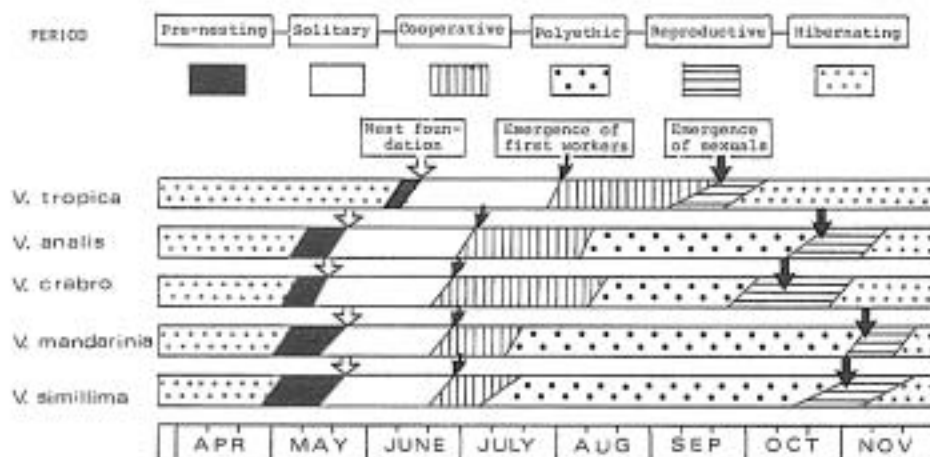


Fig. 2. Life history of five *Vespa* species in southwestern parts of Honshu, Japan.

#### 1. Pre-nesting period

This period, to be defined exactly, means a duration from the time when the queens emerge from the immobilized state of diapause to the time when they decide the sites for constructing their new nests. The dates of the first encounter of hibernated queens in the last 10 years are presented in Table 2, which shows that the time of appearance is different in each species. Judging from Table 2, together with other observations

Table 2. Date of the first encounter of hibernated queens of *Vespa* species in and near Kibi.

Species	Year									
	'66	'67	'68	'69	'70	'71	'72	'73	'74	'75
<i>V. simillima</i>	Apr.12	Apr.5	Apr.10	Apr.29	Apr.15	Apr.20	Apr.17	Apr.20	Apr.14	Apr.18
<i>V. mandarinia</i>	" 8	" 22	" 6	" 11	" 26	" 12	" 24	" 30	" 18	" 27
<i>V. crabro</i>	" 28	" 25	May 2	" 21	May 5	May 3	" 24	May 2	" 25	May 2
<i>V. analis</i>	May 3	May 5	" 2	May 9	" 3	" 5	May 9	" 7	May 8	" 2
<i>V. tropica</i>	Jun.8	" 22	" 22	Jun.4	Jun.8	" 25	" 25	" 29	" 24	" 26

by me, *V. simillima* first came out of their hibernacula each year in early to late April. Both *V. mandarinia* and *V. crabro* generally appeared from mid-April to early May, *V. analis* in early May and *V. tropica* at and after the end of May. Thus, the interspecific order of spring appearance is, *simillima* - *mandarinia* - *crabro* - *analis* - *tropica* (MATSUURA 1971).

Among these species *V. simillima* occasionally visits flowers of *Camelia japonica*, but other species seldom frequent flowers. The most important food source of post-hibernating queens is the sap of *Quercus* trees, which are particularly preferred by *V. mandarinia*, with the peak of visits from late April to early May as shown in Fig. 3. The queens take tree sap not only during the daytime but also in the evening for several

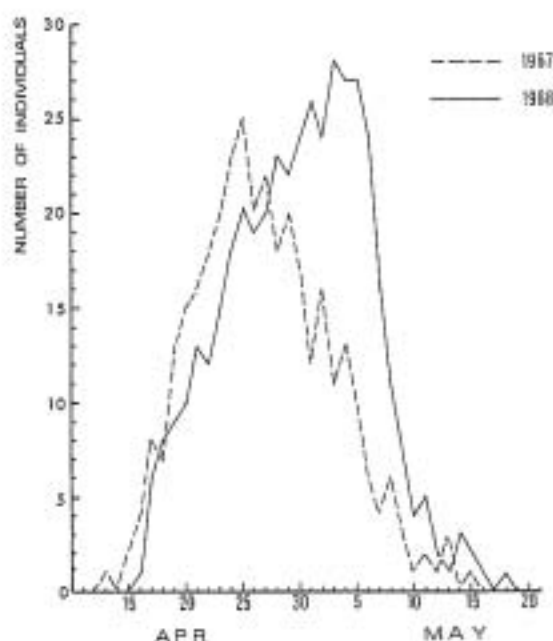


Fig. 3. Daily change of the number of overwintered *Vespa mandarinia* queens visiting tree sap in the evening at a corpse, consisting of about 20 trees of *Quercus* spp., in Kibi-cho.

days after hibernation. A distinct linear dominance relationship is recognized among these queens visiting tree sap and the intra- and interspecific relationships will be discussed in greater detail later (chap. III. Feeding habits). It has never been observed that the species of *Vespa* catch insects for food before founding their nests, in spite of my careful observations.

It is recognized that the fresh weight of post-hibernating queens of *Vespa* is very much lower than that

of the pre-hibernating ones. In *V. mandarinia* the mean fresh weight of queens was  $3.46 \pm \text{s.d. } 0.21\text{g}$  just before hibernation, and that of 34 queens collected in the spring of both 1966 and 1967 was  $2.14 \pm \text{s.d. } 0.22\text{g}$  (MATSUURA 1966).

It seems likely that such a remarkable decrease of fresh weight is closely related to their consumption of fat body during, and soon after, hibernation. The hibernating queens retain a good quantity of fat body covering the ovary within their abdomen. The amount of fat body is already small soon after departure from hibernacula and decreases rapidly with the commencement of their activities. According to SPRADBERY (1966), fat content as a percentage of the dry weight in queens of *Vespula* species is over 40 per cent, of which 30 per cent is utilized during hibernation. The quantity of fat contained in post-hibernating *Vespa* queens no longer increases in spite of their feeding activity and little fat body is observed after May (MATSUURA 1966).

## 2. Solitary period

All species of *Vespa* found their colonies with a single queen, being regarded as haplometrotic. Until the emergence of the first worker, the queen engages in all duties, including nest foundation, oviposition and the progressive provisioning to the developing larvae, as is typical in most solitary wasps.

The queens search for nesting sites after spending time in taking their own nutriment for a short period. The first observation of searching for nesting sites in *V. simillima* was on May 4th, 1965, and the last observation on May 24th, 1966 and May 19th, 1967. In *V. mandarinia* which builds underground nests, I observed first on May 22nd, 1967 and May 19th, 1968, a queen repeatedly entering some ready-made burrows excavated by snakes or small rodents, and judging from their behaviour, they were searching for nesting sites. Although I have few records of the dates of the other Japanese species, an estimation may be given on the basis of the dates of first spring appearance of post-hibernating queens (Table 2) and the data on nest contents at an early stage (Table 8): *V. crabro* after early May, *V. analis* after mid-May, and *V. tropica* after late May. In general Japanese *Vespa* species start nest building later than the other Japanese social wasps such as *Polistes*, *Parapolybia* and *Vespula* (MATSUURA 1975).

It may perhaps take a queen of each species several days, even weeks, to find a suitable nesting site. As soon as she chooses a definite nest site she starts nesting activity. The principal building materials are generally wood fibres mixed with salivary secretion. The fibres used are derived from the cortex of living trees, decayed wood and rotten parts of living trees. The first step of nest construction is to make a pedicel to support a small comb. After the first comb consisting of two to four cells is built, the queen makes an envelope to cover it. Oviposition occurs almost parallel with cell construction and the first egg is laid as soon as the first cell is completed.

A single queen of each species constructs in average 35–40 cells and rears 10–15 larvae up to the pupal stage by herself. The solitary period lasts for about two months from late spring to early summer as total development times from egg to adult in the first brood requires more than 50 days. The nesting habits in this period will be discussed in greater detail below (chap. II. Nesting habits).

## 3. Cooperative period

As shown in Table 3, first workers of *Vespa* emerged from June to July in the following order: *simillima* - *crabro* - *analis* - *mandarinia* - *tropica*. The difference in peak dates was 5 to 6 weeks between *V. simillima* and *V. tropica*, though the time of emergence varied among colonies of the same species. These workers are always smaller in size than those emerging later because cells produced by queens are the smaller than any produced later in the season (Table 7).

The new workers begin to engage a variety of intranidal activities as early as their second day and perform foraging trips at 2 to 4 days old, as soon as they are properly endowed with flying ability. After the emergence of workers, the queens are still concerned with extranidal and intranidal activities for a while, though the behaviour of queens varies in both quantity and quality in the course of colony development. This period is called the cooperative period. In this stage queens first cease their extranidal activities, then intranidal activities except for oviposition. The process will be discussed later in detail (chap. VI. Division of labour).

It seems likely that the larger the typical colony size the shorter the cooperative period lasts. In *V. tropica*,



Table 3. Date of the first appearance of *Vespa* workers in and near Kibi.

Species	Year									
	'66	'67	'68	'69	'70	'71	'72	'73	'74	'75
<i>V. simillima</i>	Jun.19	Jun.14	Jun.10	Jun.8	Jun.12	Jun.9	Jun.9	Jun.11	Jun.14	Jun.10
<i>V. crabro</i>	" 22	" 28	" 25	" 22	" 28	" 24	" 25	" 27	" 27	" 21
<i>V. analis</i>	" 10	" 14	" 20	" 16	" 23	" 13	" 20	" 23	" 23	" 20
<i>V. mandarinia</i>	" 23	" 29	" 24	" 21	" 24	" 24	" 19	" 22	" 20	" 21
<i>V. tropica</i>	Jul.24	Jul.20	Jul.24	Jul.25	Jul.23	Jul.21	Jul.26	Jul.24	Jul.15	Jul.20

which has the smallest colony size among Japanese *Vespa* species, the queens participated in intranidal tasks throughout their life. The queens of *V. analis*, which also belong to a small colony type (Fig. 65), continued to engage in internal activities for about 7 to 8 weeks after the emergence of workers. On the other hand, in the case of species of the relatively large colony type, the queens gave up their "worker tasks" after 6 to 7 weeks in *V. crabro* and 2 to 4 weeks in *V. mandarinia*. And in some colonies of *V. simillima*, which often has more than ten thousand cells, the queens stopped their intranidal activities 2 to 4 weeks after the emergence of workers.

In contrast with the next polyethic period, the colony in this cooperative period is characterized by slow development and a small number of workers as shown in Figs. 65–76.

#### 4. Polyethic period

As the number of workers increases, the queens of all species except for those of *V. tropica* become restricted to oviposition, leaving workers all the other duties. With the attainment of division of labour between queen and workers, the life of *Vespa* shifts from the cooperative period to the polyethic period, and the colony undergoes a rapid increase in population. This expansive stage lasts until the time when males and new queens emerge.

Towards the middle of this period, colonies of both *V. simillima* and *V. crabro* often relocate their nests from their original nest sites in small spaces to new, more spacious sites. This strategy is restricted to the two species mentioned and a detailed account of this remarkable feat is given in the next chapter.

In the course of this period *Vespa* workers start to display obvious attraction to their queen. They cluster around the queen on the comb, orientating towards the head and thorax (Fig. 4). Some of them continually antennate and lick her body, which is very similar to the royal court in honeybees. The phenomenon is explained by the presence of a queen substance, which has been chemically extracted from the queen of *V. orientalis* by ISHAY et al. (1965). This behaviour is not seen in the colonies of *V. tropica*, which has the smallest colony size among Japanese *Vespa* species. At the end of the season workers of *V. crabro* start to bite their queen frequently and even cause her death. But the situation in three other species, *V. analis*, *V. simillima* and *V. mandarinia*, is somewhat different, for there have been no observations of workers licking the queen violently. Queens of *Vespa* (excepting *V. tropica*) are characterized by a hairless and polished body in this period (MATSUURA 1968), which may be brought about by the licking of workers.

As the end of this period approaches, the workers of each species cease to build small cells to rear workers and begin to build cells of a larger size to produce sexuals, though the change in the size of cells appears to take place somewhat gradually. As the large cells in all the Japanese *Vespa* species (except for *V. tropica*) are always built soon after the appearance of a royal court of workers in the colony, the initiation of large queen cells appears to be controlled by the queen pheromone as already pointed out in *V. orientalis* by IKAN et al. (1969). In *V. tropica*, workers are apparently unaffected when close to their queen and not gather round her, which suggests that queen control of the workers is done in other ways. At any rate, the brood of sexuals in *Vespa* colonies are reared during the time when the worker population is at its peak, as discussed later in chap. V. Population dynamics.

The duration of the polyethic period seems to be closely related to the length of colony life in each species,

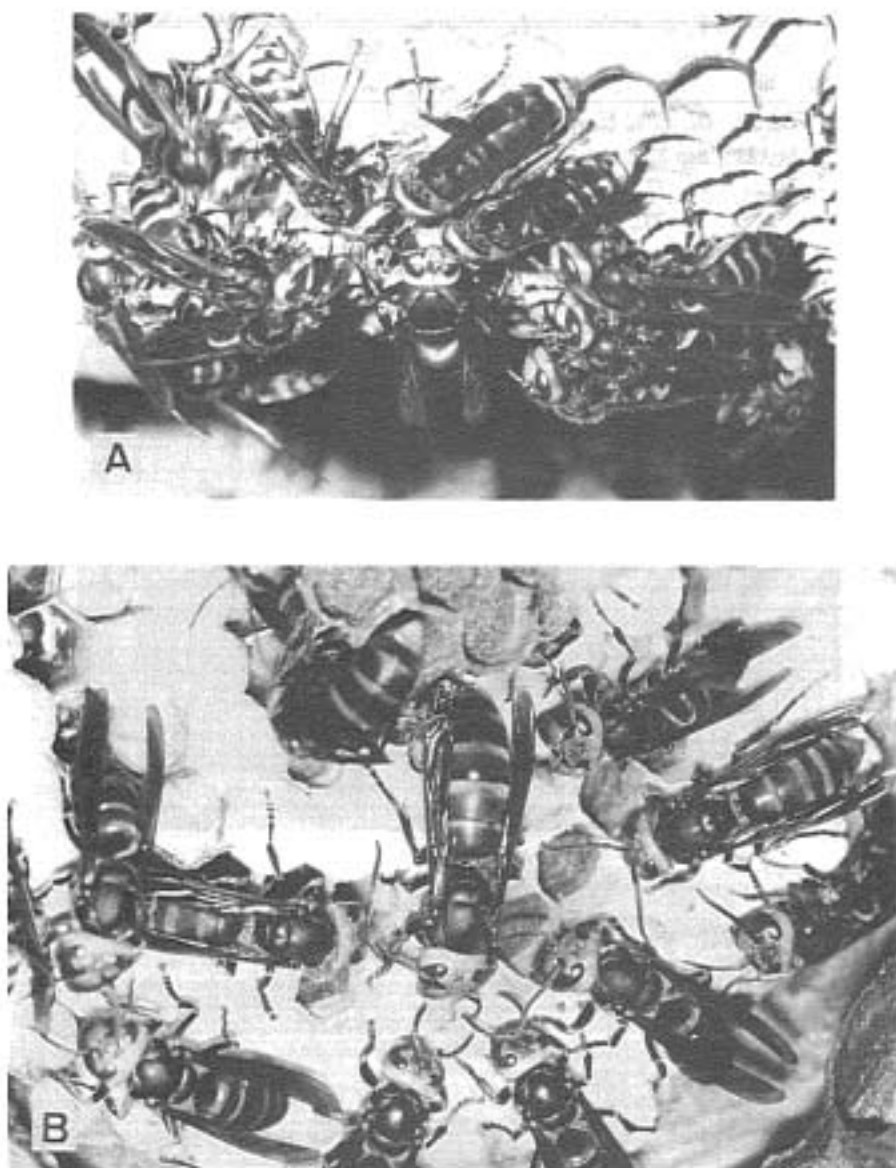


Fig. 4. Royal court in *Vespa* species: A, *V. crabro*; B, *V. analis*.

in such a way that the longer the period, the later the emergence of sexuals occurs. The period lasts 3–3.5 months in the most long-lived colonies of both *V. mandarinia* and *V. simillima*, 2–2.5 months in the moderate colonies of *V. analis*, and 1.5–2 months in the short-lived colonies of *V. crabro*.

##### 5. Reproductive period

The polyethic period comes to an end with the death of the founding queen, which usually occurs just before or soon after the emergence of sexuals. The reproductive period lasts as long as worker hornets are still alive to feed the new sexuals.

Records of the survival of founding queens observed in field-collected nests of each species are shown

Table 4. Latest date founding queens were observed in field-collected nests of *Vespa* species in and near Kibi.

Species	Year									
	'66	'67	'68	'69	'70	'71	'72	'73	'74	'75
<i>V. simillima</i>	Oct.20	Oct.12	Nov.3	Nov.11	Nov.7	Oct.27	Sep.27	Oct.10	Oct.23	Sep.3
<i>V. crabro</i>	Sep.22	Sep.22	Oct.19	Oct.15	—	Sep.30	" 19	" 3	" 17	—
<i>V. analis</i>	—	" 17	Sep.17	" 22	—	" 24	" 13	Sep.1	Sep.11	Oct.6
<i>V. mandarinia</i>	—	" 20	Nov.1	—	—	Oct.18	Oct.10	" 24	—	" 7
<i>V. tropica</i>	—	—	Aug.30	Sep.25	Aug.29	Sep.18	Aug.27	—	—	Aug.26

Fig. 5. New queens of *Vespa crabro*: A, resting in the cells; B, resting on the envelope.

in Table 4. The queens of *V. tropica*, a short-cycle species, died towards late August, whereas those of both *V. mandarinia* and *V. simillima*, long-cycle species, survived even to November. The interspecific order of disappearance of founding queens is, *tropica* - *crabro* - *analis* - *mandarinia* - *simillima*, which is in accordance with the order of emergence of new queens. The life span of queens in each species appears to be about one year.

With the death of a founding queen the colony enters a disorganized state. Some workers fight one another, and nest development ceases, though foraging activity and brood nursing continue. After 3-4 days, the colony recovers the lost harmony in parallel with the appearance of laying workers. A detailed account is given in chap. IV. Division of labour.

The males and new queens emerge at the same time, or the former a little earlier than the latter towards the disorganized stage of the seasonal cycle (cf. chap. VIII. Population dynamics). With the appearance of sexuals the expansion of the nest structure is stopped or considerably reduced. Sexuals remain 10 to 20 days within the nest, and spend most of their time thrusting head and abdomen into empty or egg-containing cells at the centre of the comb (Fig. 5) except for occasional food intake from workers (Fig. 6) and larvae.



Fig. 6. *Vespa tropica* new queens soliciting a worker for salivary secretion.

They have nothing to do with the division of labour in the colony. At the later stage of this period foraging activity of workers changes principally from protein food to carbohydrates such as tree sap, fruit juice, etc., to feed the adult males and new queens. This results in a decrease in attention to the larvae, which fail to be fed and remain in the same instar for several weeks before finally dying. The death of the last surviving workers brings about the complete disintegration of the colony. The last sexuals to emerge cannot obtain sufficient food. They leave the nest without maturing and all die of hunger around the nest. On the other hand, fully matured sexuals whose body colour has intensified and body weight has increased (e.g., from 2.9g to 3.5g in *V. mandarinia*, MATSUURA 1966) depart from their nests. Departing sexuals do not make an orientation flight and never return to their nest.

The disintegration of colonies ordinarily takes place from early September to late November in the following order: *tropica* - *crabro* - *analis* - *simillima* - *mandarinia*. Thus, the duration of the reproductive period lasts about a month in each species.

#### 6. Hibernating period

The males of *Vespa* fly about for a few weeks after leaving the nest, visiting flowers, tree sap and some mushrooms, whereas the new queens leave straight away probably searching for a hibernaculum. Mating occurs

around the nest entrance in *V. mandarinia* and elsewhere away from nests in other species. Only in *V. mandarinia* do males visit nests and await departing queens at the entrance to copulate with them (Fig. 7). At this time many males of *V. mandarinia* swarm in the air to seize the queens.

Hibernating queens so far discovered were found mostly within the soil or rotten wood with a high percentage of moisture as shown in Table 5. A common hibernating site for these species is in the soil overhanging



Fig. 7. Copulating in *Vespa mandarinia*.

Table 5. Hibernation sites of *Vespa* species

Species	Site in			Total
	Soil	Rotten Wood	Straw Heap	
<i>V. simillima</i>	17	59	0	76
<i>V. crabro</i>	6	0	0	6
<i>V. analis</i>	15	69	0	84
<i>V. mandarinia</i>	10	0	2	12
<i>V. tropica</i>	54	15	0	69
Total	102	143	2	247



Fig. 8. *Vespa tropica* queen hibernating in decayed wood.

cliffs in the forest. But, some queens of *V. simillima*, *V. analis* and *V. tropica* were observed hibernating within the rotten wood of old stumps or logs lying on the ground (Fig. 8). The environments of these hibernation sites are always dim and rather moist places in the forest, mostly facing to the north where the change of day and night temperature range seems to be least. The cell prepared for hibernation (or hibernaculum) and the tunnel leading to the cell are clearly dug by the queen herself and are not pre-existing ones. The inside wall of the cell is carefully finished; the soil or wood surface to which she clings is always made quite even. The tunnel is plugged with earth or wood chips from within to cut off the space from the outside.

The hibernating queen is always found clinging to the upper wall or ceiling of the cell, closely drawing her antennae and all legs to her body surface and concealing to the tips of her folded wings under the ventral surface of her abdomen. The queens always hibernate one per cell, except a single case of *V. analis*, where two queens were found in the same cell within rotten wood (MATSUURA 1966), though SANDEMANN (1936) reported



that ten queens of *V. crabro* hibernated together inside the rotten wood of a dead ash tree. These hibernating habits differ from *Vespula* (SANDEMANN 1936, DUNCAN 1939, THOMAS 1960) and *Polistes* (MATSUURA 1966) in their predominantly solitary hibernation and preparation of hibernating chambers instead of mere utilization of pre-existing cavities. The queens which enter hibernation have ovaries of very immature condition and there is a large amount of fat body covering the ovary within the abdomen (MATSUURA 1966).

The duration of the dormant period is 6 to 8 months, varying with the species of hornet; the queens of *V. tropica* spend two or three months longer in hibernation than any other species in southern Japan.

## II. NESTING HABITS

The nests of hornets are remarkable and complex structure which require a great proportion of time and energy in construction and maintenance. The early part of nest building is performed by the founding queen, but the larger part of it is accomplished by the workers.

In this chapter, aspects of their nesting habits which have many special features are discussed, together with some specific differences.

### 1. Nest sites

All Japanese species of *Vespa* are distributed in mountain outskirts and hillsides, being relatively scarce plains and in high mountains. Nests sites of *Vespa* are shown in Table 6. Based upon the data obtained from

Table 6. Nest sites of *Vespa* species.

Species		Open place					Covered place				Total
		Thicket	Bough of tree	Eaves of building	Rock wall	Other sites	Attic	Hollow tree	Other sites	Underground cavity	
<i>V. similis</i>	A*	2	0	2	0	0	24	3	8	34	73
	B**	2	8	95	13	14	39	2	3	2	178
<i>V. crabro</i>	A*	0	0	0	0	0	13	4	7	15	39
	B**	0	0	0	0	0	25	4	5	7	41
<i>V. analis</i>		149	0	13	2	0	0	0	0	0	164
<i>V. mandarina</i>		0	0	0	0	0	0	0	0	56	56
<i>V. tropica</i>		0	0	0	0	0	10	4	7	24	45

Notes: A\*, nest sites before or without relocation of nests; B\*\*, nest sites after relocation of nests.



Fig. 9. Nests of *Vespa analis*: A, young nest in the cooperative period; B, mature nest in the polyethic period.

a total of 596 nests, it is recognized that the nest site preference of *Vespa* differs characteristically with species, being classified into open place and covered place types. The specific differences are as follows: *V. analis* and *V. simillima* belong to the species of the open place preference. *V. analis* nested only in open situations above ground and 149 out of 164 nests, or 90.9%, hung from bushes or trees near the ground (Fig. 9). *V. simillima* often moves nests after worker emergence from their original sites to new locations as discussed in detail later. The queens of this species tend to initiate their nests in covered places (35/73 nests, or 50.7%) or underground cavities (34/73 nests, or 46.6%), where the microclimate is most suitable for the early stage of development. When the nest becomes too large, the whole colony moves to a new, more spacious site, and 132 out of 215 nests, or 61.4%, were attached in open places such as beams or eaves of buildings (95/215 nests, or 44.2%)(Fig. 10), though it is obvious that this species is more variable in nest site selection than any other congeneric species in Japan both before and after the relocation of nests. On the other hand, three species, *V. crabro*, *V. tropica* and *V. mandarinia*, utilize only covered situations, *V. crabro* and *V. tropica* make their nests either in restricted cavities or

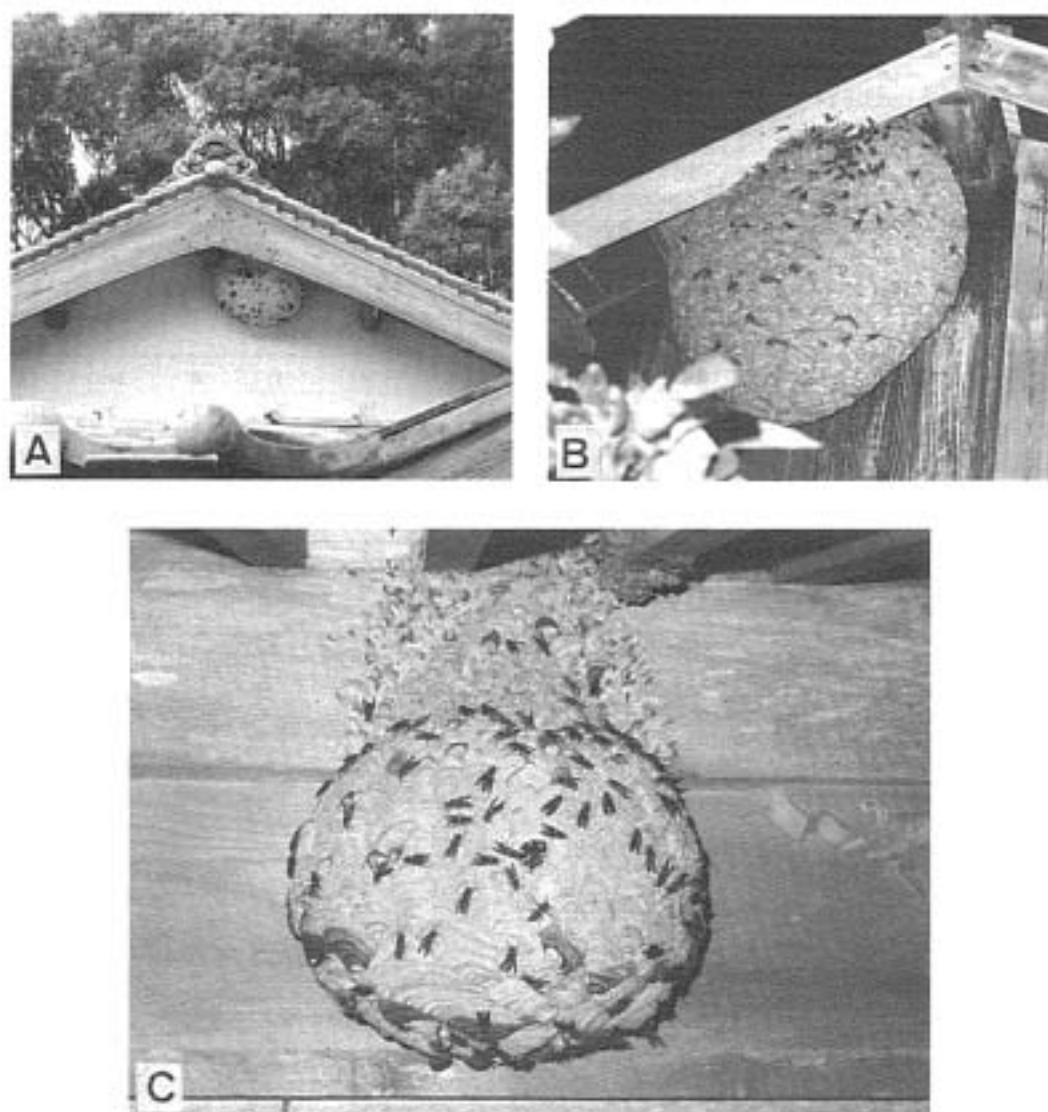


Fig. 10. Mature nests of *Vespa simillima* made under the eaves.

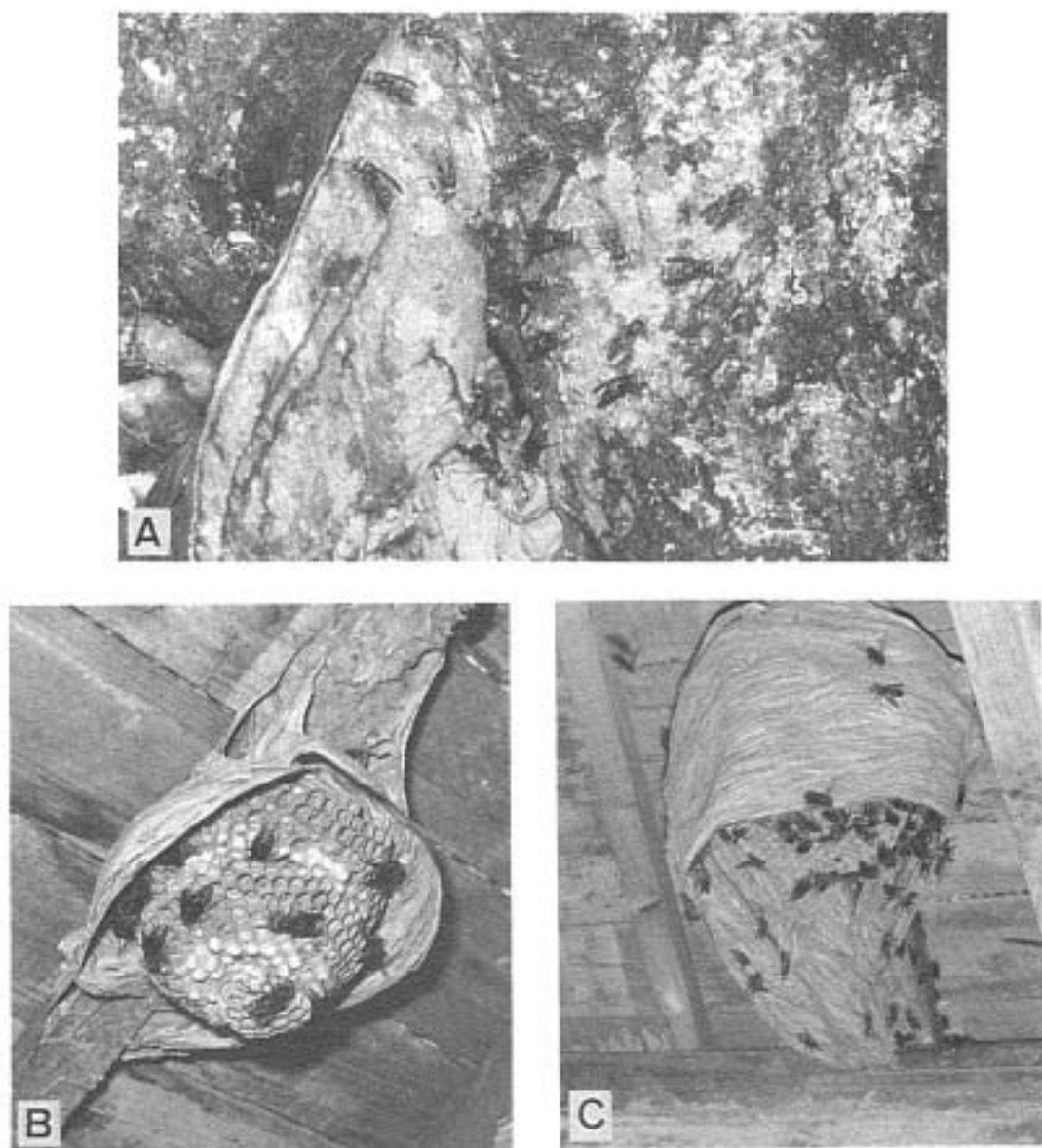


Fig. 11. Nests of *Vespa crabro*; A, nest site in hollow tree; B, young nest in attic; C, mature nest in attic.

in ample spaces both above and underground (Figs. 11 ~ 14), though the former species often moves its nest site. *V. mandarinia* nests only underground situations (Fig. 15); among 56 nests examined, 47 were found in subterranean cavities either formed around rotten pine roots or made by small rodents, snakes, etc., and 9 in subterranean tree hollows.

Height of the nest sites above the ground differs with species, *V. analis* usually builds its nest at lower levels about 2m from the ground (140 out of 164 nests, or 85.4%). On the other hand, 184 out of 215 nests, or 85.6%, of the aerial nests of *V. simillima* were built 2 ~ 7m above ground. Nests of the species group preferring covered locations, *V. tropica* and *V. crabro*, were made at lower levels within about 4.5m from the ground. Subterranean nests of four species, *V. simillima*, *V. tropica*, *V. crabro* and *V. mandarinia*, were all located

within 0.6m below the ground surface.

No particular directional preferences for nests of any of the species could be determined (MATSUURA 1971a).

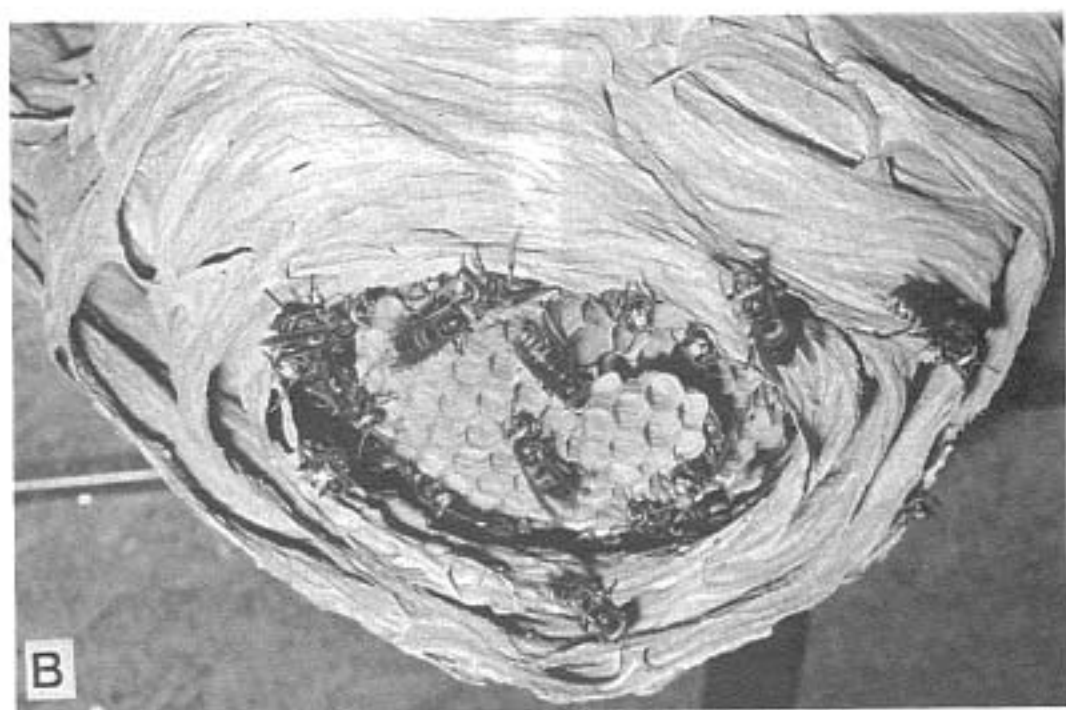


Fig. 12. Mature nest of *Vespa crubro*: A, nest in attic; B, bottom of same nest.

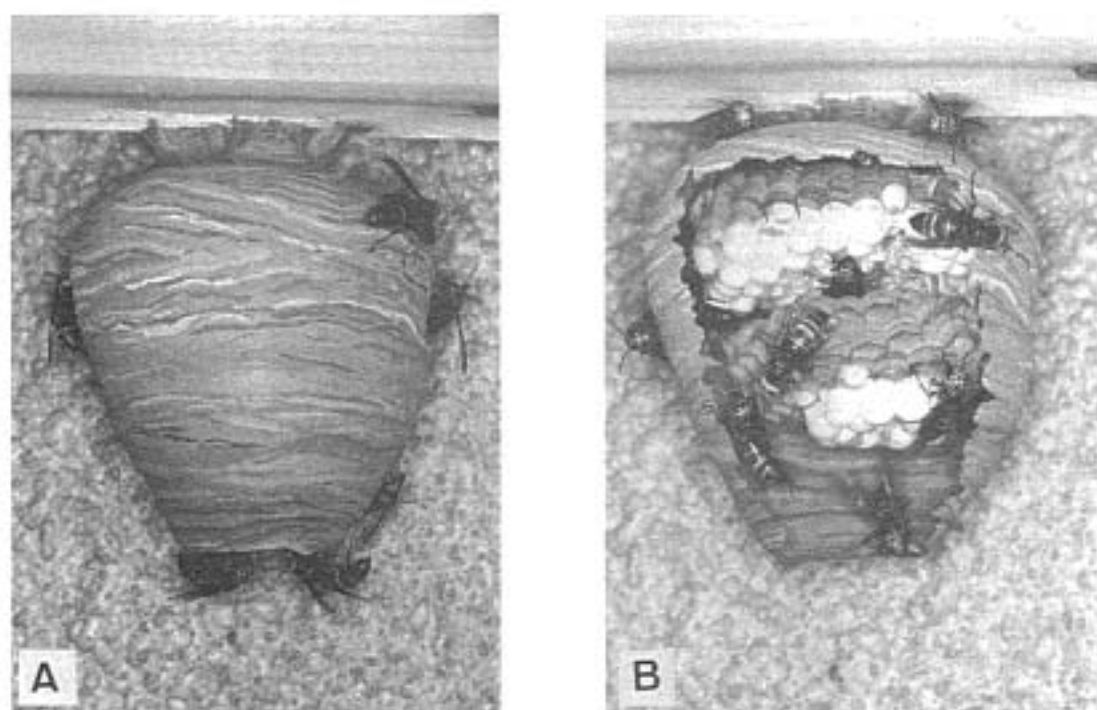


Fig. 13. Nest of *Vespa tropica*: A, mature nest; B, same nest with envelope partially removed.



Fig. 14. Nest of *Vespa tropica* underground.





Fig. 15. Nests of *Vespa mandarinia* underground: A, young nest; B, mature nest.

## 2. Nest structure

## 1) Queen nest

Concerning the nest foundation by queens of *Vespa* only a small amount of data are available on a nest of *V. analis* (A7101) which was observed from its very initiation (Fig. 16, A–D). Unfortunately, this colony

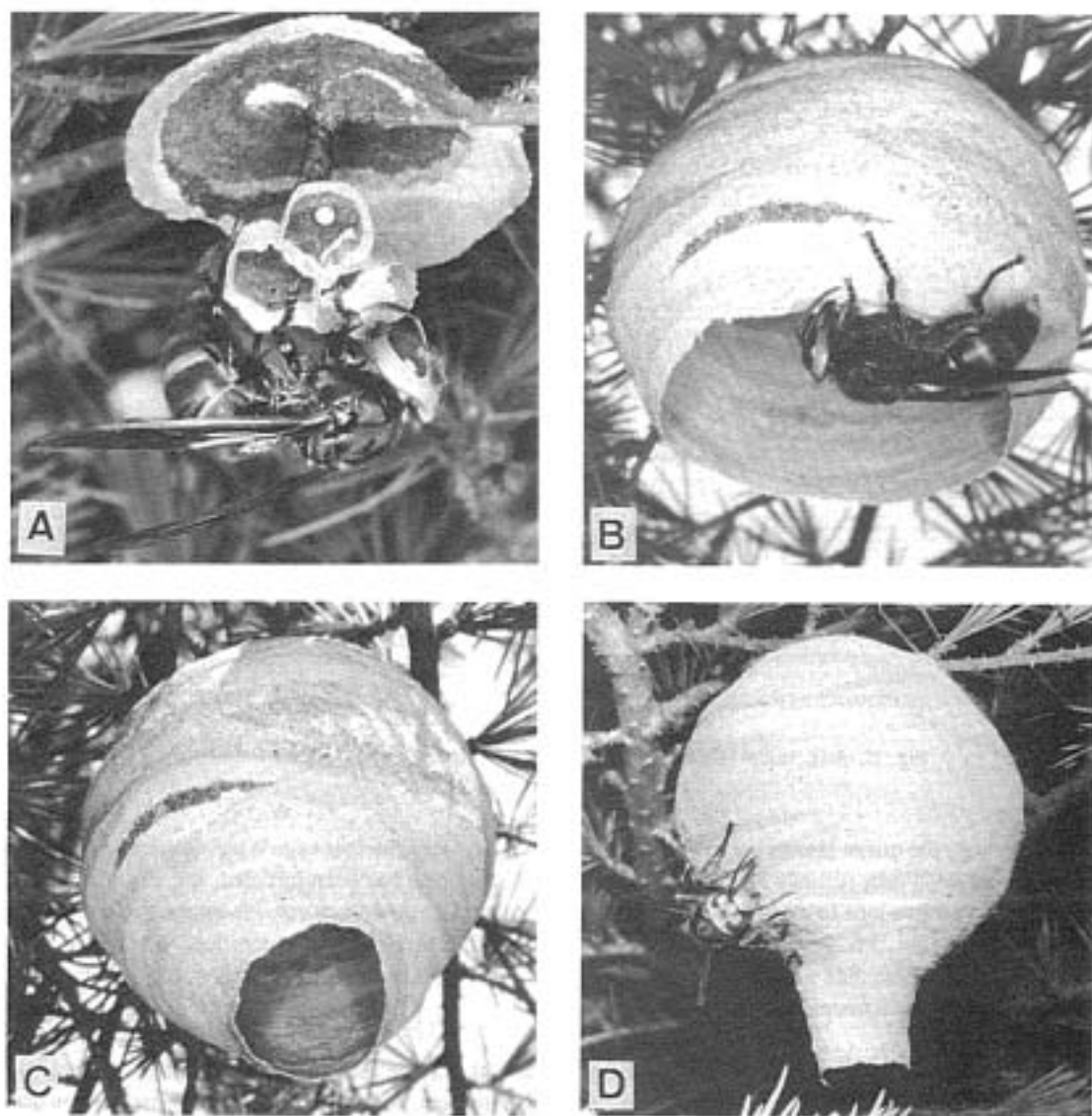


Fig. 16. A–D. Initial stages of nest building by a *Vespa analis* queen.

was orphaned by the death of the queen before the emergence of workers. Fig. 17, A–H shows some incipient nests of *V. similima* which indicate successive stages in early nest construction by queens of this species. The following description is based mainly upon the observations given in Figs. 16 and 17 together with many fragmentary observations in other species.

The first step of nest construction by a queen is to make a pedicel to support a small comb. A few loads of wood pulp are applied at one spot, from which a pedicel is made in the shape of a club, pointing sharply downward. As soon as the first cell, being circular in cross section, is completed on the tip of

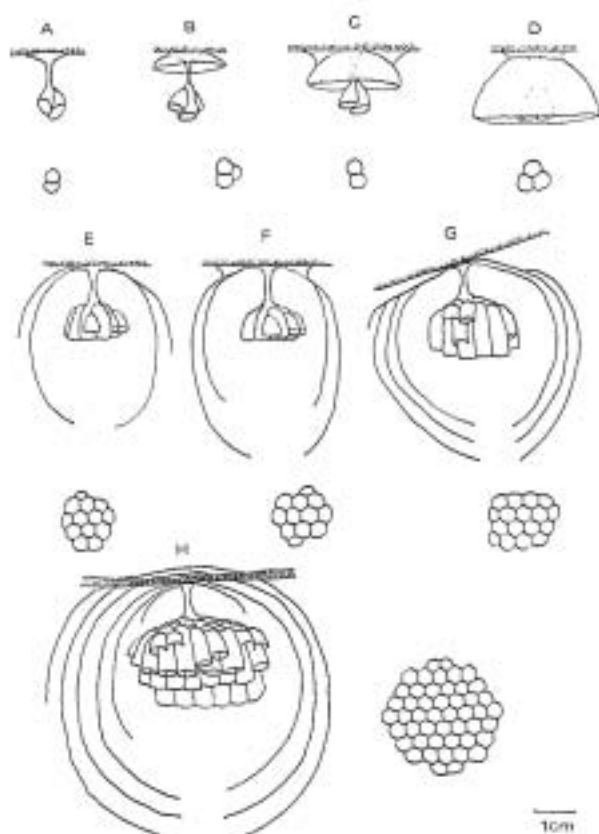


Fig. 17. A-H. Initial stages of nest building in different nests of *Vespa similima*.

the pedicel, the queen inserts her abdomen into the cell, and lays the first egg. When the first comb, consisting of 2–4 cells (usually 3 cells in *V. analis* and *V. tropica*), has been initiated, the queen begins to construct an envelope to cover it by the end of the first day. The queen nests of *Vespa* species have usually 3 to 5 cells after two days, 4 to 7 cells after five days, and 6 to 10 cells after ten days. The queen nests never contain more than a single comb and the basic features in *Vespa* are, in comparison with other genera, *Vespula* and *Dolichovespula*, as follows:

a) Pedicel

In *Vespa* nests the pedicel is made centrally never laterally as in some *Polistes*, and the comb always assumes a horizontal position as in the other vespine wasps. The pedicel, which is firmly fixed to prevent the nest from being swung, is in the shape of a club, like that of *Polistes* wasps, and strengthened by painting a lustrous substance on its surface. On the other hand, the queens of both *Vespula* and *Dolichovespula* first construct a triangular hanging sheet of paper (ORMEROD 1868, DUNCAN 1939, BRIAN and BRIAN 1948, SHIDA 1959). From the centre of the lower edge of this suspending sheet a thin downward-pointed spindle with a slight spiral twist is built, and a comb of cells is hung from the tip of the spindle. According to SHIDA (1959), "the triangular plate-like stalk" which is used in *Vespula flaviceps* usually has a 90–180° twist and effectively absorbs the impact given to the nest when the comb is swung.

b) Cell

In *Vespa* species, the cells constructed by queens are always smaller in size than those constructed

Table 7. Sizes of the nests of *Vespa* species.

Species	Builder	Suspensoria		Worker cell			Thickness of envelope	No. of nests observed
		Length	Thickness	Diameter	Depth	Thickness		
<i>V. simillima</i>	Queen	7.6 ± 0.7*	2.3 ± 0.5*	7.7 ± 0.2*	24.3 ± 2.4*	0.18 ± 0.09*	0.34 ± 0.8*	12
	Worker	7.3 ± 0.9	18.6 ± 17.5	9.1 ± 0.9	24.4 ± 2.5	0.28 ± 0.06	0.48 ± 0.4	10
<i>V. crabro</i>	Queen	9.1 ± 0.6	1.9 ± 0.7	8.5 ± 0.3	25.3 ± 1.6	0.24 ± 0.05	0.23 ± 0.6	6
	Worker	8.8 ± 0.5	10.6 ± 9.7	9.4 ± 0.9	28.9 ± 3.2	0.29 ± 0.05	0.34 ± 0.7	11
<i>V. analis</i>	Queen	7.6 ± 0.4	2.7 ± 0.7	7.3 ± 0.5	23.5 ± 3.1	0.24 ± 0.07	0.48 ± 0.9	15
	Worker	7.2 ± 0.6	14.7 ± 9.9	9.8 ± 0.5	25.2 ± 4.6	0.33 ± 0.09	0.58 ± 1.1	10
<i>V. mandarinia</i>	Queen	15.8 ± 1.1	3.4 ± 0.5	10.5 ± 1.7	31.6 ± 4.7	0.31 ± 0.08	0.85 ± 1.2	5
	Worker	18.9 ± 9.8	5.4 ± 4.8	12.6 ± 2.1	34.2 ± 3.1	0.40 ± 0.09	1.05 ± 0.7	10
<i>V. tropica</i>	Queen	17.0 ± 1.2	2.3 ± 0.6	7.8 ± 1.2	23.2 ± 2.3	0.28 ± 0.07	0.68 ± 0.4	9
	Worker	17.6 ± 1.8	6.4 ± 3.4	10.3 ± 1.8	23.6 ± 3.3	0.32 ± 0.05	0.78 ± 1.5	10

\*: Mean ± s.d.

later by workers, and also both cell walls and envelope are distinctly thinner as shown in Table 7. Since cell size directly affects the brood development, the larvae reared in such small cells emerge as the smallest individuals throughout the season. No conspicuous difference in the forms of cell and comb are exhibited either intra- or intergenerically among *Vespa*, *Vespula* and *Dolichovespula* at this stage of development.

The number of cells built by a single queen of *Vespa* species is shown in Table 8. These results, along with other observations on many deserted nests, indicate that in all the Japanese species of *Vespa*, a single queen constructs on average 35–40 cells and rears 10–15 larvae up to the pupal stage by herself. No marked difference is noticed among the various species. On the other hand, JANET (1903) recorded a queen nest of *Vespa crabro* containing 60 cells all occupied by brood, of which 13 larvae had been reared to pupae. As far as I am aware, this is the maximum number of cells made by a single queen in all the *Vespa* nests so far studied. Two queens of *Vespa orientalis* reared by DARCHEN (1964) made respectively 16 and 14 cells under laboratory conditions. In *Vespula* species SHIDA (1959) described a nest of *Vespula flaviceps* with 40 cells, and DUNCAN (1939) recorded a probably incomplete nest of *Vespula pensylvanica* with 12 and another of the same species with at least 17. In *Dolichovespula* the same author reported a nest, presumably of *D. maculata*, with 18 cells, and BRIAN and BRIAN (1948 and 1952) cited six nests of *D. sylvestris* with 15, 21, 31, 33, 37 and 42 cells, respectively. Judging from these records, though still insufficient both in numbers of nests and species observed, it seems reasonable to conclude that the number of cells founded by queens of *Vespa* species does not markedly deviate from that of *Vespula* and *Dolichovespula*.

#### c) Envelope

The envelope is started from the substratum, or the base of the pedicel, never in the middle of the pedicel. Specific differences in the form of envelopes are distinctly shown among queen nests. The form of the completed envelope can be divided into the following three types; bowl-shaped, ball-shaped and flask-shaped.

**Bowl-shaped type:** This type has an inverted bowl-like envelope which never completely encloses the comb. *V. tropica* (Fig. 19) and *V. mandarinia* (Fig. 18) build this type; the envelope of the former is 5.0–5.5cm in diameter and that of the latter 7.0–7.5cm.

**Ball-shaped type:** This type has a roughly spherical envelop completely enclosing the comb except for a small hole left at the bottom. *V. crabro* (Fig. 20) and *V. simillima* (Figs. 17 and 21) build nest of the same type, though the number of sheets constructed varies with the species. *V. crabro* always builds an envelope composed of a single sheet. While *V. simillima* (Fig. 17) builds a second and third sheet, even sometimes a sixth sheet. The envelope of *V. crabro* measures 6.8–8.5cm in diameter at its widest part, and that of *V. simillima* 4.4–4.6cm inside and 7.5cm outside.

Table 8. Nest contents and number of cells in *Vespa* species at the incipient stage.

Species	Date	Empty cells	Eggs	Larval instar					Cocoons	T. no. of cells	No. of adults	
				1st	2nd	3rd	4th	5th			♀	♂
<i>V. similima</i>	May 23'69	1	3	0	3	3	0	7	0	17	1	0
	May 27'70	0	10	4	0	0	0	0	0	14	1	0
	Jun. 3'71	3	6	4	3	5	1	13	13	48	1	0
	May 26'73	0	9	4	0	0	0	0	0	13	1	0
	Jun. 24'75	2	12	4	3	3	2	12	5	43	1	4
<i>V. crabro</i>	May 27'69	2	2	1	1	1	5	13	6	31	1	0
	May 29'75	3	2	6	3	3	4	6	2	29	1	0
<i>V. analis</i>	May 29'68	2	11	4	1	2	0	0	0	20	1	0
	Jun. 8'68	4	8	2	2	1	2	4	0	23	1	0
	Jun. 13'68	0	8	4	4	2	3	6	8	35	1	0
	Jun. 8'69	3	8	1	3	2	0	0	0	17	1	0
	Jun. 12'69	1	4	1	3	1	2	11	7	30	1	0
	Jun. 2'71	5	5	3	3	1	3	4	0	24	1	0
	Jun. 2'71	2	3	0	4	0	0	2	2	13	1	0
	Jun. 2'71	0	3	1	5	0	0	7	5	21	1	0
	May 27'72	2	11	3	0	3	0	0	0	19	1	0
	Jul. 21'72	2	7	1	3	3	3	11	7	37	1	2
	Jul. 28'72	2	0	3	5	3	2	17	12	44	1	4
	May 30'73	0	11	3	3	2	3	1	0	23	1	0
	Jul. 15'73	2	10	1	2	2	3	8	9	37	1	0
	Jul. 15'73	0	26	3	1	3	5	17	14	69	1	4
	Jun. 26'75	7	11	1	1	1	1	9	10	41	1	4
<i>V. mandarinia</i>	Jun. 25'67	—	—	—	—	—	—	—	—	37*	—	—
	Jun. 29'68	—	—	—	—	—	—	—	—	40*	—	—
	May 10'73	1	19	0	0	0	0	0	0	19	1	0
	Jun. 30'75	—	—	—	—	—	—	—	—	40*	1	0
<i>V. tropica</i>	Jun. 12'68	2	15	0	0	1	0	5	0	23	1	0
	Jul. 21'68	7	2	0	0	0	0	6	2	17	1	0
	Jul. 21'68	2	8	2	1	2	2	12	12	41	1	0
	Jul. 25'73	3	25	2	2	3	5	3	9	52	1	2
	Jul. 13'74	2	10	2	2	1	3	12	11	43	1	0
	Jun. 19'75	0	16	0	0	0	0	0	0	16	1	0
	Jul. 17'75	10	11	0	0	0	0	4	10	35	1	0

\* Deserted nest.

*Flask-shaped type*: This has a cylindrical spout at the bottom of the envelope composed of a single sheet (Fig. 22). In the Japanese species, *V. analis* and *V. affinis* build this type; the form of the spherical part of the envelope is slightly variable. Of 42 incipient nests of *V. analis* collected from 1964 to 1975, the diameter at the spherical part was 7.4cm in the largest nest and 6.1cm in the smallest one (on average 6.6cm  $\pm$  s.d. 0.6cm). The cylindrical vestibule is built before the first larva begins to spin its cocoon and is not rebuilt if destroyed. In both ball-shaped and flask-shaped types (Figs. 16 and 22) the nests in the course of construction vary gradually in the shape of the envelope from a plate-shaped envelope at the beginning to the final form described above, because queens tend to build cells and envelope more or



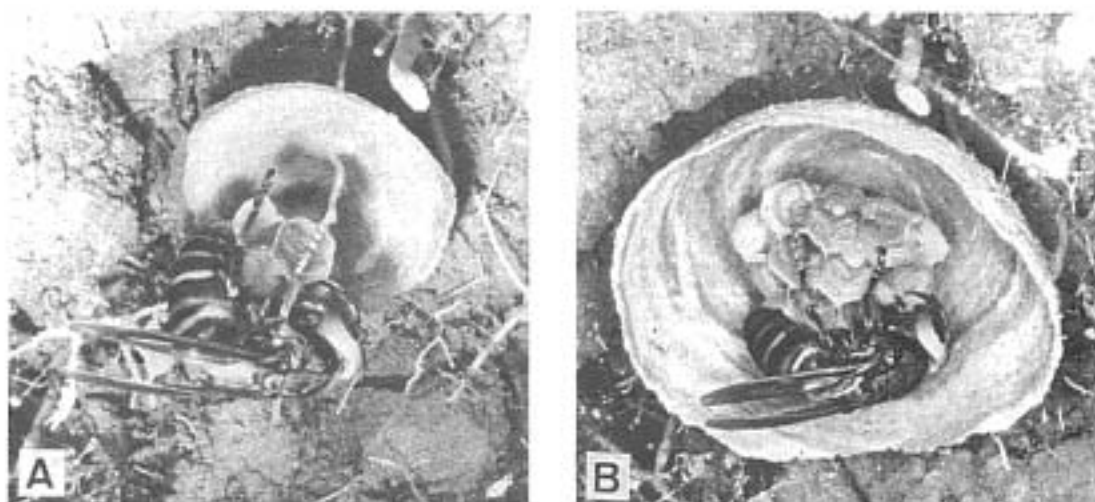


Fig. 18. Initial stages of nest building by a *Vespa mandarinia* queen.

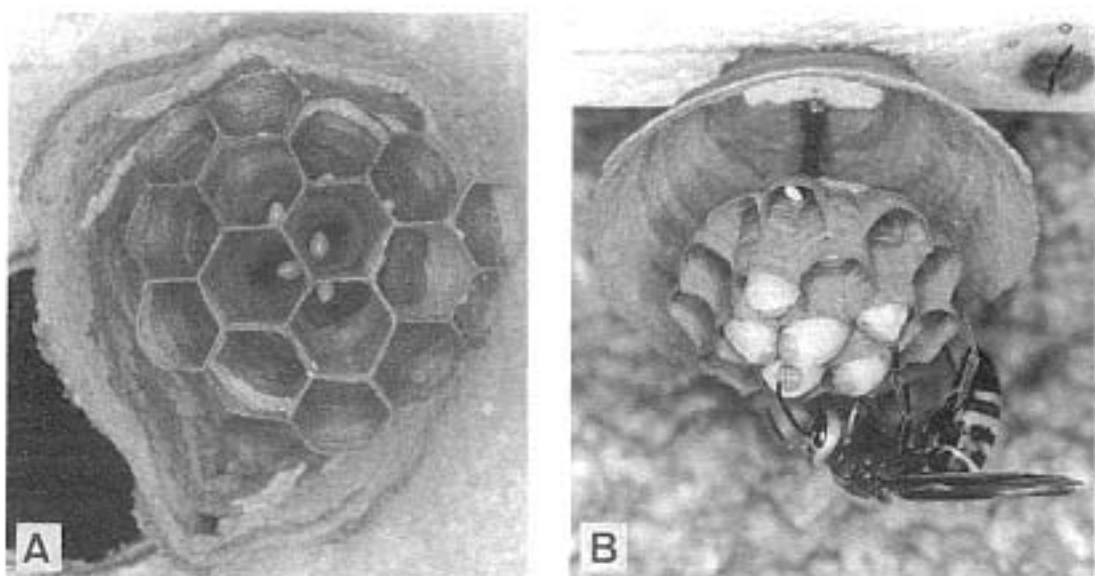


Fig. 19. Queen nests of *Vespa tropica*.

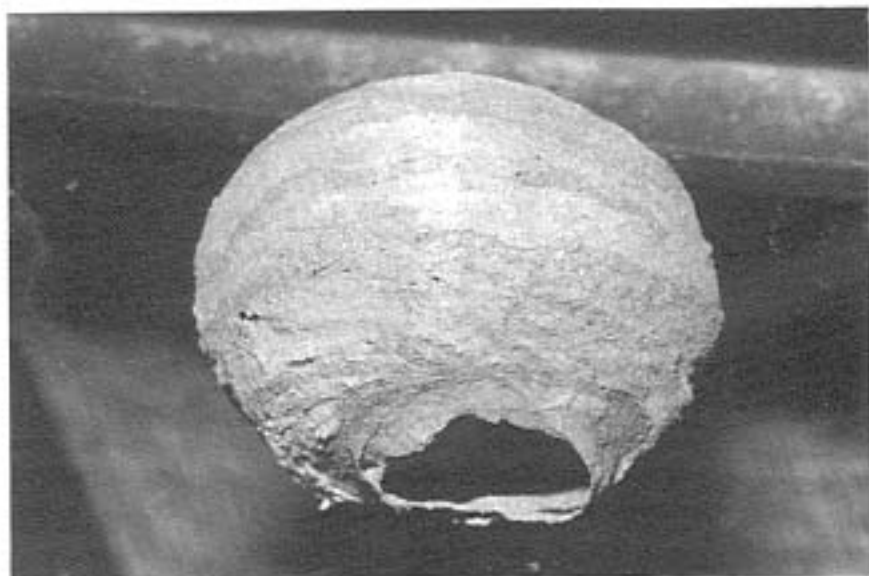


Fig. 20. Queen nest of *Vespa crabro*.

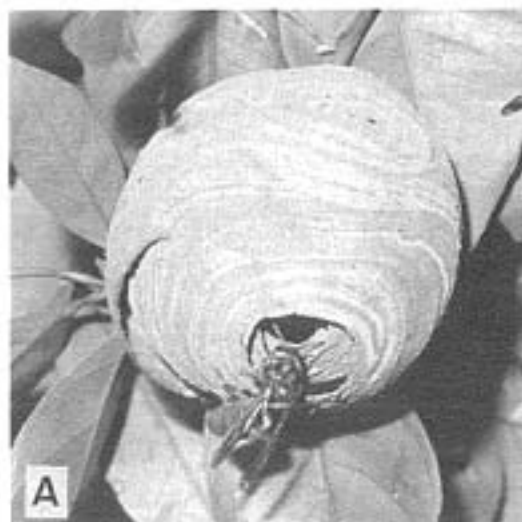


Fig. 21. Queen nests of *Vespa similima*.

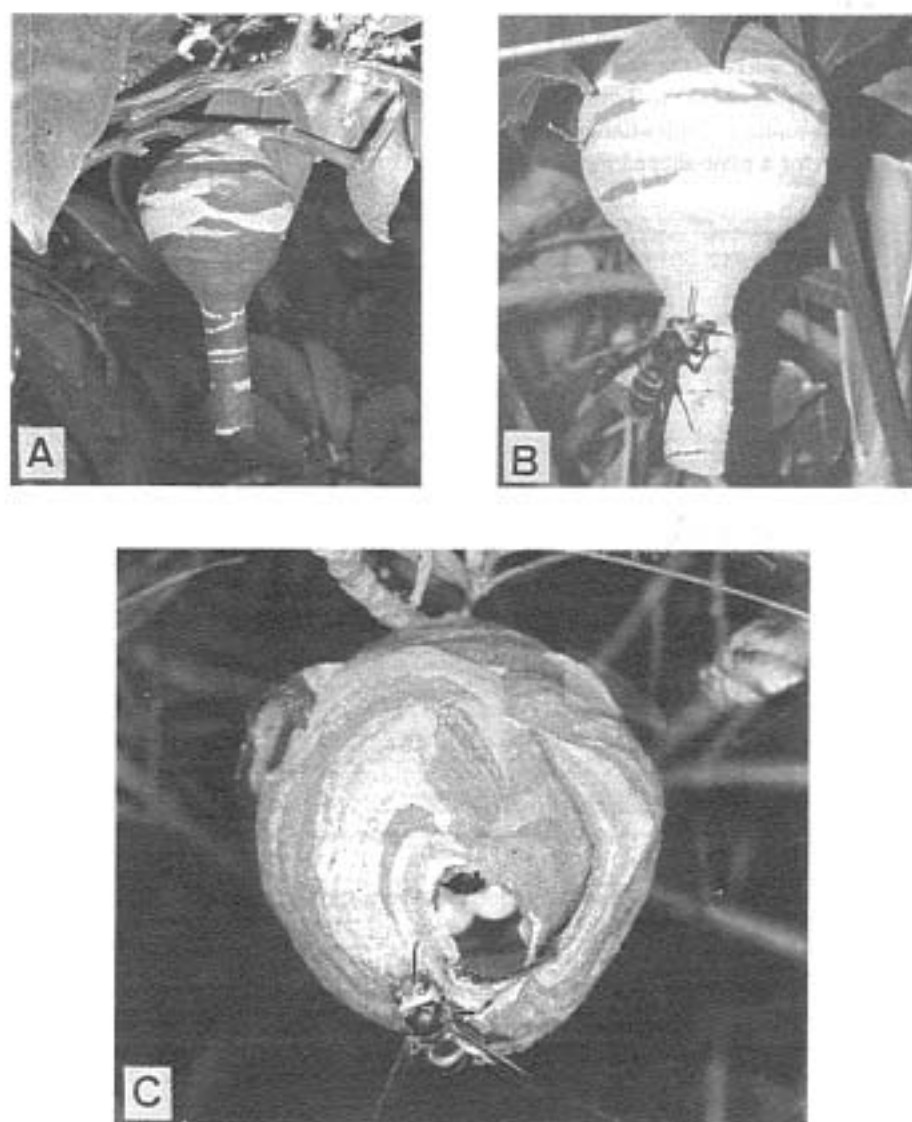


Fig. 22. Nests of *Vespa analis*: A, B; complete queen nests with a tubular vestibule; C, nest after the workers have removed the tubular vestibule.

less simultaneously until reaching the final stage.

2) Change in nest shape with the emergence of workers

After the first workers emerge, the shape of the envelope changes and quickly loses the characteristic nest shape. In *V. similina* when the workers begin adding new scale-like layers on the outside, they also tear away the inner layers made by the queen to make cells for the enlargement of the comb. The first few layers inside the nest are chewed away until only a disc-like remnant remains above the comb, in contrast to *Dolichovespula* nests, where the envelope remains composed essentially of separate layers of paper (DUNCAN 1939). In *V. analis* the workers make no additions to the cylindrical vestibule at the bottom of the envelope built by the queens. After four or five workers have emerged, this tubular passageway is completely removed by the workers and is not

reconstructed (Fig. 22.C). The envelope is enlarged by the addition of new scales on the outside by workers and the entrance is shifted from a ventral position to a position in the direction which affords the easiest access to foraging workers. On the other hand, the workers of *V. tropica* and *V. mandarinia* build an additional wall layer down to the first envelope constructed by the queen, and remnants of early envelopes remain above the topmost comb without any disturbance by workers. *V. crabro* workers take off the original envelope except for a plate-shaped part left at the base of attachment (Fig. 23), and this form is main

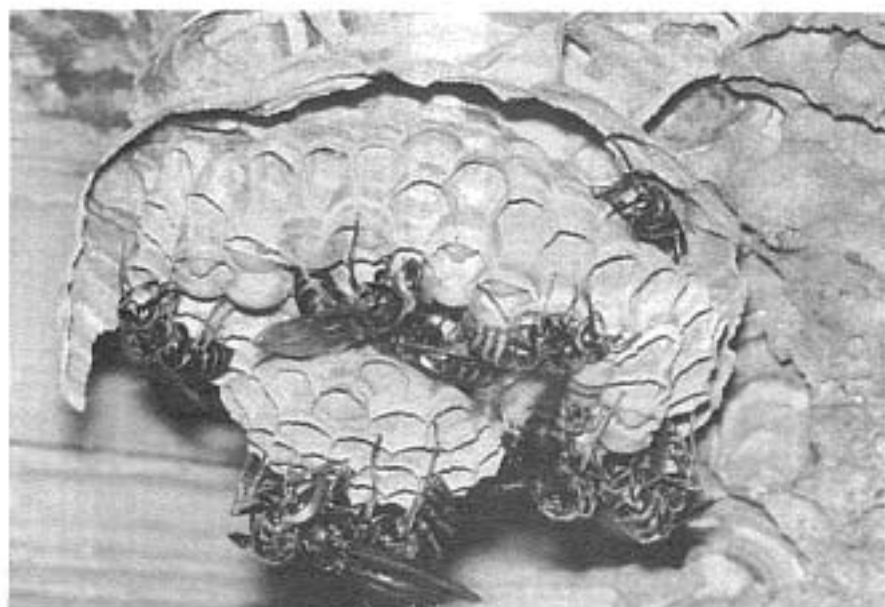


Fig. 23. Young nest of *Vespa crabro*.

tained until the end of July. Such treatment seems to be a specific character of this species.

### 3) Developed nests

SAUSSURE (1853–1855) divided the nests of social wasps into two primary types, gymnodomous and stelocytarous. Vespine nests belong typically to the latter type which is enclosed in an envelope and contains several combs suspended one below the other and without connection, with the envelope. Mature nests of *Vespa* exhibit certain specific differences in nest structure. Basic features are described below.

#### a) Pillar

In *Vespa* nests except for *V. analis* each comb is connected to the others by one main pillar (0.8–2.0cm long) and 2–50 auxiliary pillars. In the nest of *V. analis* the first comb always hangs from the support by one pedicel and additional combs are also hung from the earlier one by a pedicel. As nests of all *Vespa* species are enlarged and their weight increases, additions to the pedicels are made by plastering paper pulp on them and on the adjacent surfaces of the combs. This treatment thickens the pedicels and broadens their bases. In the case of *V. simillima* the size of pedicels built above the first comb reaches 5–9cm in thickness.

#### b) Cells

The average size of brood cells in *Vespa* species is given in Table 7. The size of worker cells is ranked as *mandarinia* - *tropica* - *crabro* - *analis* - *simillima*, though the cells for workers and sexuals are different even in each species. In all Japanese species cells built by the queen are used 2–3 times; usage only once or more than three times is so far unknown. In combs built by workers, cells of the upper combs are used 2–3 times and of the lower ones 1–2 times. But even in the tip comb some peripheral incomplete cells appear to be unused, judging from the absence of cocoon residues.

### c) Combs

In three species, *V. mandarinia*, *V. analis* and *V. tropica*, the dorsal surface of each comb is conical and higher at the centre. The surface is rough and the bottom of each cell is easily recognized, contrasting to the horizontal combs with flat, even dorsal surfaces in *V. crabro* and *V. simillima*. In *V. mandarinia* the synchronous building of a few primordia and their later fusion forming a single comb is not rare, but in the other four species a new comb starts always from a single central primordium which is gradually expanded concentrically if not obstructed.

The number of combs per nest at a late active period is 4–7 in *V. mandarinia*, 7–10 in *V. simillima*, 6–7 in *V. crabro*, 3–4 in *V. analis* and 2–3 in *V. tropica*. The top comb of *V. mandarinia* and *V. tropica* is abandoned after summer, after which it is attacked by moulds, whereas *V. crabro* and especially *V. analis* and *V. simillima* strengthen the tip comb by filling empty brood cells with exogenous materials and utilize it as a strong support for the lower combs. The largest combs so far measured were 61.0 × 48.0 cm with 1,191 cells in *V. mandarinia* (S6403), 39.0 × 38.5 cm with 1,177 cells in *V. simillima* (S6403), 40.5 × 40.0 cm with 1,468 cells in *V. crabro* (C7307), 16 × 16 cm with 250 cells in *V. analis* (A7522), and 14.0 × 11.5 cm with 155 cells in *V. tropica* (T7105), respectively.

### d) Envelope

The general shape of the envelope changes between the species of the open place preference and those of the covered place preference as stated earlier. In the first group with *V. simillima* and *V. analis* the envelope is usually thick, covering the nest completely. In developed nests of these species the envelopes consist of multi-layered shell-like sheets involving many aerial chambers between them. In the case of *V. simillima* the thickness of envelope in a large nest reached 3.5–5.5 cm at the middle and 12 cm at the bottom. On the other hand, the second group with *V. crabro*, *V. tropica* and *V. mandarinia* the envelope consists of only a few plate-like sheets with imperfect aerial chambers, and the lowest comb is always exposed within the nest cavity.

### e) Nest entrance

Normally all the nests of *Vespa* have only one entrance hole. The nests of *V. simillima* and *V. analis* have a single circular opening shifting in position from the bottom of the nest to the side at a very early stage; usually the entrance in old nests is relatively high up on the nest wall. On the other hand, the species building in covered places, such as *V. mandarinia*, *V. crabro* (Fig. 12) and *V. tropica* (Fig. 24), always

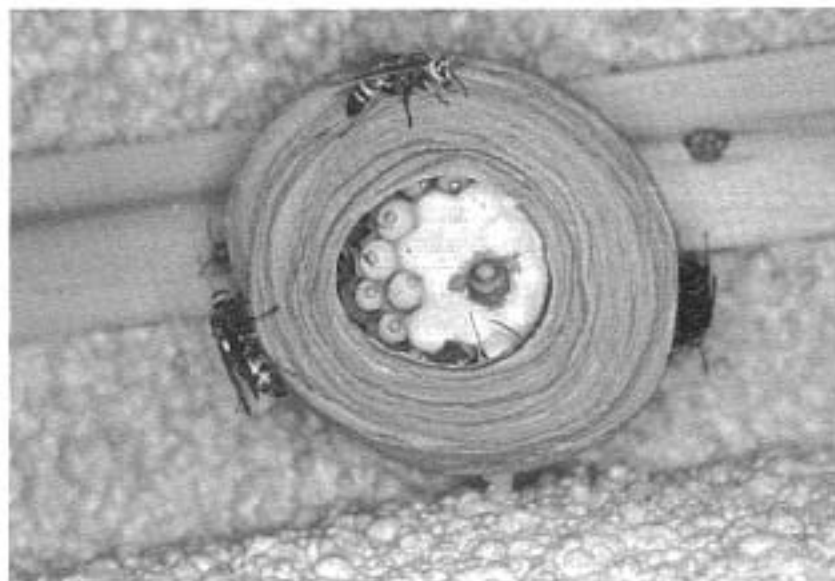


Fig. 24. Nest entrance of *Vespa tropica*.



omit the envelope at the bottom of the nest and the workers utilize the opening as an entrance hold. In subterranean nests the pre-existing burrow connecting the cavity and ground surface is used as the entrance canal with the length varying from 2 to 60cm.

In *V. crabro* crevices around the nest are fully stuffed with wood pulp, which attained in a highly developed case 5m in length and 20cm in width. Such treatment seems to be a specific character of *V. crabro*, though the workers of *V. tropica* and *V. mandarinia* also build a few rudimentary seals at the entrances to nests.

### 3. Modification of nest site

After the emergence of workers a nest site requires a certain amount of modification to adapt it to the needs of a growing colony. *V. mandarinia* queens which prefer rather narrow cavities under ground, do a great deal of excavating to enlarge the cavity in which the nest is built. Nest cavities are extended as soil adjacent to the nest envelope is constantly removed and taken away from the nests. The workers remove soil particles and make a small ball with their mandibles. Keeping the ball between the mandibles, they leave the nest on foot and drop the ball close to the entrance. At the peak of nest expansion a tongue-like platform of removed soil appears at the entrance, which, in a highly developed case, attained 2m in length, 50cm in width and 15cm in maximum depth. Stones too large to be moved are dropped to the bottom of the nest cavity by the removal of the earth beneath them. On the contrary, in *V. tropica*, which builds the smallest nest among Japanese hornets, a relatively wide space in the covered place is chosen as their nest site, so that there is always a space between the wall of the nest and that of the cavity. *V. analis* does very little work upon the nest site because the queen nests only in open situations above ground, though the workers clear away leaves and twigs around the nest when the nest is built in dense foliage. On the other hand, both *V. simillima* and *V. crabro*, when nesting in narrow cavities, usually abandon the original nest sites and relocate the colonies without gnawing the walls of the cavities to enlarge them. A detailed account on this phenomenon is given in the following section.

### 4. Relocation of nest

As stated in the previous section *V. simillima* belongs to the species of the open place preference. As to the queen nest, however, it is clear that the queen prefers a concealed site (Table 6), though is more variable in nest site selection than any other congeneric species in Japan. In this species 30 out of 50 nests (60.0%) built by the queen were relocated to a different locality when the nests had attained large size and required more space for comb building. Among the nests of *V. simillima* observed after late July from 1964 till 1975,

Table 9. Date of first observation of relocating colonies of *Vespa simillima* and *V. crabro*.

Species	Year								
	'65	'66	'67	'68	'70	'71	'72	'73	'75
<i>V. simillima</i>	—	—	Jul.20 (S6701)	Jul.26 (S6801)	Aug. 8 (S7003)	Jul.17 (S7106)	Jul.15 (S7201)	Aug. 2 (S7304)	Jul.22 (S7503)
<i>V. crabro</i>	Aug.12 (C6502)	Jul. 1 (C6601)	—	Jul. 2 (C6801)	Aug.27 (C7002)	Aug.17 (C7101)	Aug.27 (C7201)	Aug. 9 (C7301)	—

132 out of 149 nests (88.6%) were such relocated nest. In *V. crabro*, whose queen builds only in concealed situations, 24 out of 45 nests (53.3%) observed after July from 1966 till 1975 were also relocated from the original nesting site. On the other hand, I have not observed such relocation of nests in the other three species, *V. analis*, *V. tropica* and *V. mandarinia*. The relocated nests were observed in mid-July to early August in *V. simillima* and in early July to late August in *V. crabro* as shown in Tables 9 and 10. The nests with many brood suggest that relocation had begun earlier than the observed times. Judging from Tables 9 and 10, and other observations on many nests so far observed, it seems that the queens leave their original nest from late June in both species.

Table 10. Colony composition and related data for original and relocated nests of *Vespa similima*.

Nest code	Nesting site	Distance between nests (m)	Date	No. of		No. of empty cells	No. of eggs	No. of larvae					No. of cocoons		No. of adults		
				Cells	Cells			1st	2nd	3rd	4th	5th	♀	♂	♀	♂	♂
O-ST105	Underground cavity	32	Jul.17'71	3	331	35.0	0	0	0	0	0	64	24	0	0	92(3)	0
R-ST106	Attica		Jul.17'71	3	368	0.5	147	32	33	24	39	72	19	0	1	66(0)	0
O-ST207	Wooden box	10	Jul.31'72	2	1,350	18.6	173	64	58	60	68	236	440	0	0	293(8)	0
R-ST208	Eaves of building		Jul.31'72	2	94	52.1	45	0	0	0	0	0	0	0	1	76(0)	0
O-ST214	Cavity under roofing tiles	6	Aug.17'72	2	234	72.6	11	13	2	0	0	16	37	0	0	18(0)	0
R-ST214	Eaves of building		Aug.17'72	3	400	0.8	186	8	21	29	16	88	0	49	0	101(0)	0
O-ST302	Underground cavity	12	Jul.25'73	2	194	39.2	0	0	0	0	0	46	72	0	0	20(0)	0
R-ST307	Eaves of building		Aug. 7'73	3	281	2.8	2	0	21	17	13	66	154	0	1	22(0)	0
O-ST402	Underground cavity	4	Sep.16'74	3	941	57.0	36	0	2	5	15	158	187	0	0	190(8)	0
R-ST401	Eaves of building		Sep.16'74	5	2,115	77.0	446	46	85	23	2	1	0	28	1	140(0)	232

\* O: Original nest. \*\* R: Relocated nest. ♀: Foundress queen. Figures in parentheses denote stylotized workers.

Based upon the records of about 150 nests of both *V. similima* and *V. crabro* observed from 1965 to 1975, the process of relocation of the nest is illustrated schematically in Fig. 25. Workers begin to search for new site when the space becomes too narrow for their nest. Scout workers fly in all directions in search of a new permanent nest site. As already pointed out the workers of *V. similima* select aerial situations in most cases, whereas those of *V. crabro* always search for concealed situations for their new nest site. When a suitable site is found not far from the original nest the scout settle on the place and spend most of their time at rest there (Figs. 26.A and 27.A). They only occasionally return to the original nest. Different scouts settle on different sites simultaneously, and a contest ensues. Selection of a nest site is continued for several days and at the most suitable site the number of workers increases during the period. With the commencement

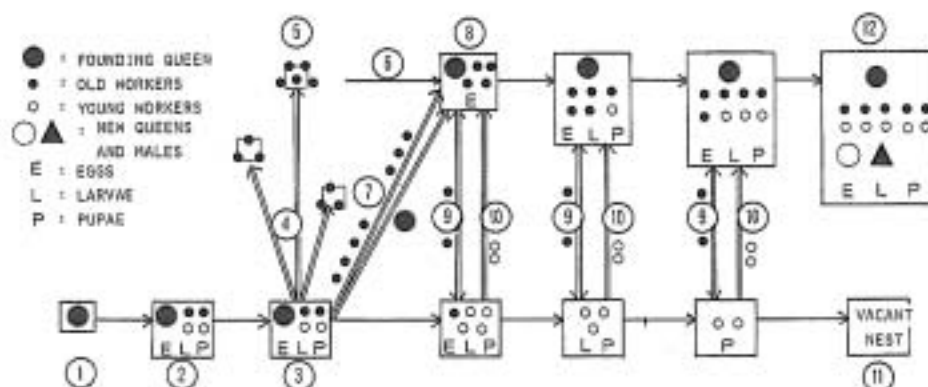


Fig. 25. The process of relocation of colonies in *V. similima* and *V. crabro*.

1. Nest foundation by queen in narrow cavity. 2. With the growth of the colony, the nest requires more available space. 3. Scout workers begin to search for a new nest site near the original nest. 4. When a suitable site is found the scouts settle on different sites and a contest ensues. 5. Selecting a nesting site continues for several days. 6. The number of workers increases at the most suitable site. 7. The old workers and the queen leave independently to search for the new nest site. 8. About a day after arrival of the queen the workers start building a new comb and the queen lays eggs. 9. Most of the workers in the new nest frequently visit the old nest to feed the remaining larvae and young workers until they leave. 10. Newly emerged workers search for their new nest. 11. The original nest is abandoned when no brood remain to be fed.

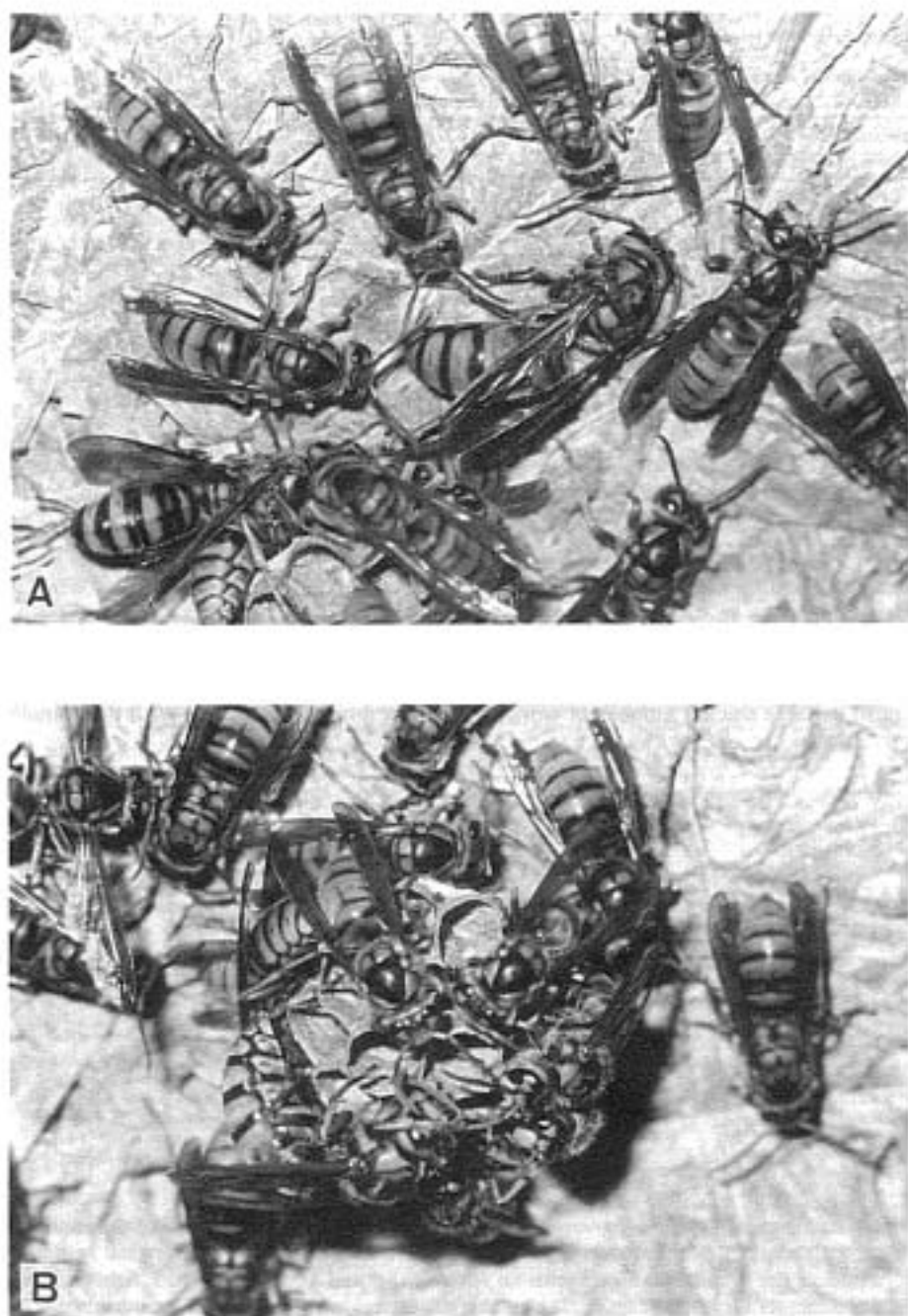


Fig. 26. Nest relocation in *Vespa similima*: A, workers and the queen gathering at a new site; B, construction of new cells.

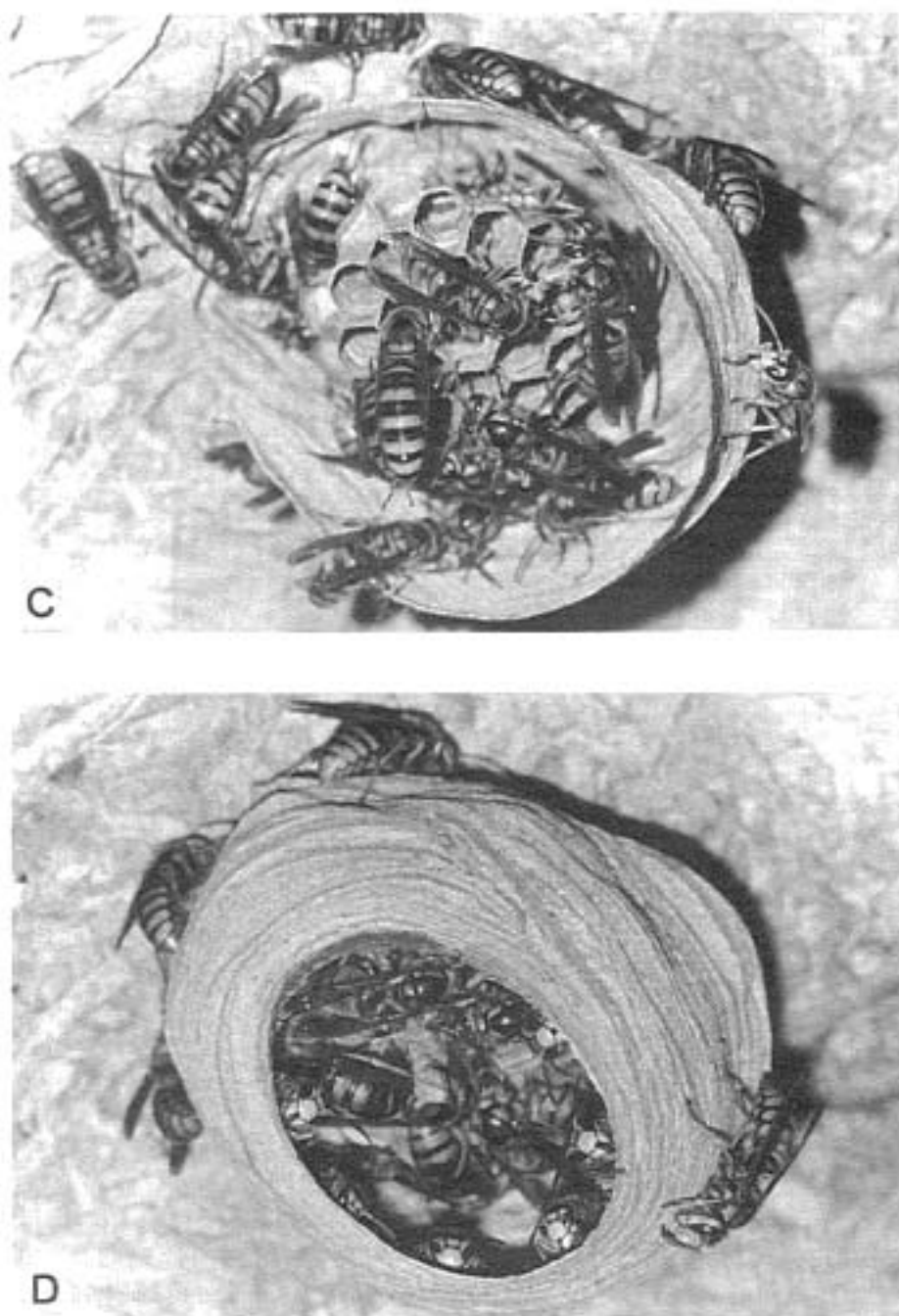


Fig. 26. Nest relocation in *Vespa simillima*: C, nest with a rudimentary envelope; D, nest with a spherical envelope enclosing the first comb.

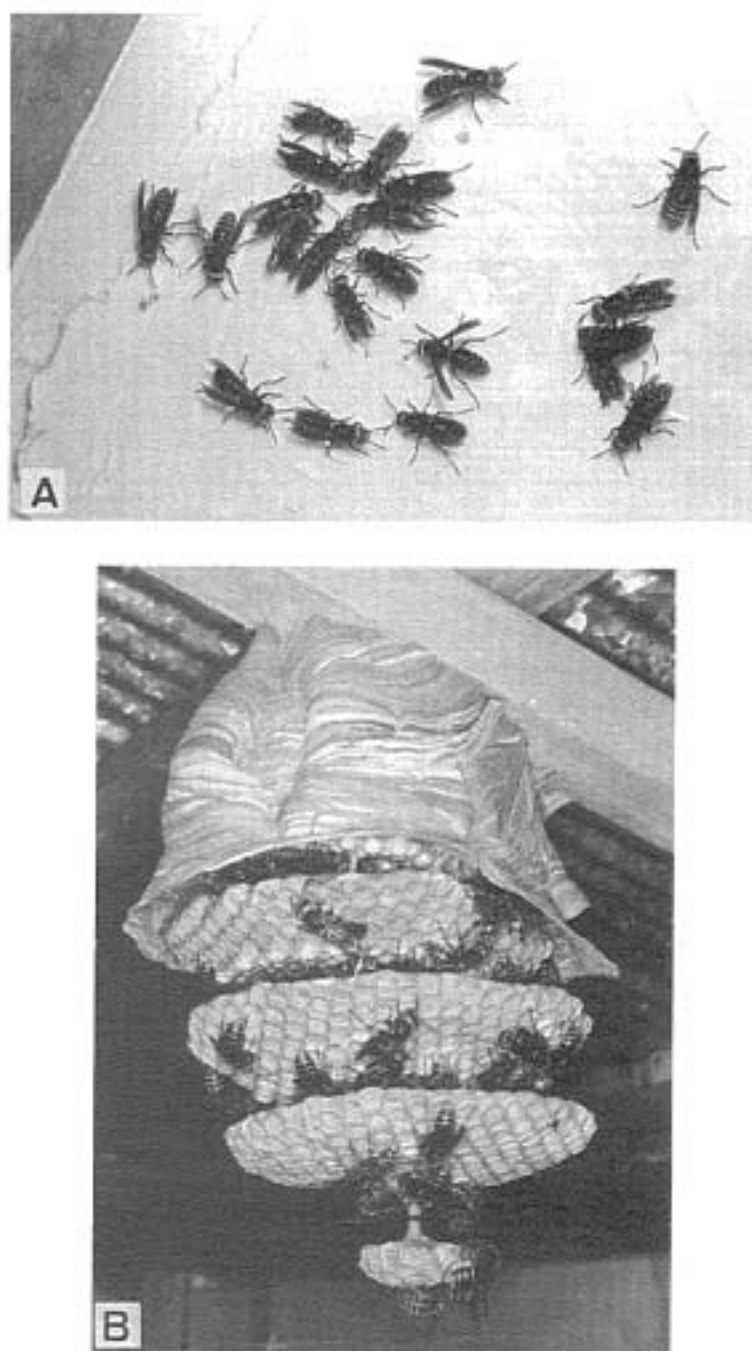


Fig. 27. Nest relocation in *Vespa crabro*: A, workers gathering at a new site; B, completed nest.

of searching for a new nest site, workers in the original nest cease building activities and the queen stops ovipositing. Then she leaves on her own to search for the new nest site. About a day after arrival of the queen the workers start building a new nest. As soon as the first comb consisting of five to twelve cells, without



an envelope, is constructed the queen begins to lay an egg in each cell (Fig. 25.B). Within several days workers commence to build a roughly spherical envelope composed of a single sheet (Fig. 25.C) and cover the comb completely except for a small hole at the bottom (Fig. 25.D). The second comb is built after the first one is completely covered with envelope. The queen stays at the new nest and never engages in extranidal activities.

Now there are two colonies usually 10m or less apart (although the maximum recorded was 180m). The fraction remaining at the original nest contains young workers and brood, and the fraction at the new nest contains older workers and the queen without larvae and pupae. In addition to their tasks in the new nest, most of the workers frequently visit the old nest to feed larvae and newly emerged workers until they leave independently for the new nest. Thus, the workers emerging in the old nest perform orientation flights when two or three days old (probably as soon as they are endowed with flying activity) and then start to search for the relocated nest. Thus relocation usually lasts for about a month until the majority of brood mature and move from the old nest to the new one. In the case of *V. simillima* the date of the last observation of relocating workers was August 9th in 1971(Nest S7109) and August 29th in 1968(Nest S6704). With the emergence of workers in the new nest the original one is abandoned because there is no longer any brood to feed.

The descriptions given above suggest some bionomic characters specific to *V. simillima* and *V. crabro* which cause them to vacate old sites and construct new nests elsewhere, this behaviour may be caused by the limited space in the original nesting site. As already stated, the queens of these species prefer rather narrow cavities at the time of nest foundation (Table 6) and the workers scarcely extend the cavities. In contrast, *V. mandarinia* workers constantly remove the soil adjacent to the nest and deposit it away from the nest. The reason that the queens of these two species select such narrow spaces for their primary nest sites seems to be related to their relatively early appearance and nest foundation (Tables 2 and 3): the microclimate in the soil or in the small cavities appears to be close to ideal for brood development in the early nesting stage. Furthermore, colony emigration in these species is not particularly precarious undertaking because the brood left in the old nest are reared successfully by workers located to the new nest. With the relocation of the nest, the colony can enter the expansion phase of its cycle in the new site with more space.

On the other hand, some social wasps and bees are also able to vacate old, unfavourable sites and construct new nests elsewhere, which is called "absconding". The brood cannot be moved in this case, and it is left behind to die. In the meliponine bees, absconding is a rare and especially precarious undertaking. When it occurs, as reported in *Trigona* by PORTUGAL-ARAUJO (1963), for example, the queen must be left behind since she is unable to fly, and the colony must produce a new queen and see her successfully through her nuptial flight in order to survive.

## 5. Thermoregulation

The regulation of nest temperature is a general capability of the social insects. In *Vespa* colonies, when workers are absent or few during the early part of the season, the queens and workers rarely perform thermoregulation and the temperature of the nest approximates that of the surroundings (Table 11). With the development of the colony and the building of thicker envelopes, the presence and the activity of the numerous adults and larvae in the nest causes a certain elevation of the nest temperature as compared to that of the surrounding environment. From early summer to autumn, colonies are able to regulate their temperature as shown in Table 11 and Fig. 28. In the colonies of *Vespa* species the temperature within the colony usually stayed close to 32°C during most of the summer days and ca.30°C during early autumn. The diurnal range of nest temperature on a day in early September was 29.9 ~ 30.6°C in *Vespa simillima* and 28.5 ~ 30.2°C in *V. analis* as illustrated in Fig. 29. According to ISHAY et al(1967) a nest of *V. orientalis* in the ground with a temperature of 28.5°C fluctuated less than one degree centigrade despite an external variation of 10 ~ 39°C. HIMMER (1932) stated that the internal nest temperature of *Vespula vulgaris* remained almost always between 29.5°C and 32°C though the outside temperature averaged 18.5°C during the observation period. These data indicate that temperature control in wasp colonies is less constant and uniform than the 35°C of a honeybee colony which fluctuates less than 0.5°C during the active season (GATES 1914, HIMMER 1932, LINDAUER 1954).

The regulation of nest temperature is attained in several ways. The elevation of nest temperature is

Table 11. Nest temperature maintained by some colonies of *Vespa* species.

Species	Date	Temp.(°C) of		No. of adults	Nest site
		Nest	Outside		
<i>V. simillima</i>	May 26 '73	21.2	20.1	1 ♀	Inside bee hive
	Jul. 9 '71	29.9	26.2	1 ♀, 92 ♂	Eaves
	Aug. 19 '71	31.8	27.4	1 ♀, 326 ♂	Eaves
	Sep. 15 '71	30.0	23.0	1 ♀, 875 ♂	Underground
	Oct. 5 '70	30.8	20.6	{ 1 ♀, 1,047 ♂ 7 ♀, 199 ♂	Eaves
<i>V. mandarina</i>	May 10 '73	22.3	22.3	1 ♀	Underground
	Jun. 29 '75	24.5	24.1	1 ♀, 3 ♂	Underground
	Jul. 17 '74	26.3	23.1	1 ♀, 14 ♂	Underground
	Oct. 31 '67	32.0	17.3	102 ♀, 50 ♂	Underground
	Nov. 25 '67	31.6	16.7	{ 87 ♀, 134 ♂ 283 ♂	Underground
<i>V. crabro</i>	Aug. 9 '73	31.8	24.7	29 ♂	Underground
	Sep. 17 '67	32.0	25.5	120 ♂	Underground
<i>V. analis</i>	May 29 '68	22.2	21.7	1 ♀	Thicket
	Jul. 8 '68	26.5	24.2	1 ♀, 8 ♂	Thicket
	Aug. 20 '73	31.4	28.3	90 ♀, 4 ♂	Thicket
	Sep. 24 '68	30.9	22.3	1 ♀, 60 ♂, 11 ♀	Thicket
	Oct. 14 '67	27.6	16.4	39 ♀, 36 ♂	Thicket
	Nov. 4 '71	19.8	10.3	33 ♂	Thicket
<i>V. tropica</i>	Jun. 12 '68	23.2	23.0	1 ♀	Underground
	Aug. 8 '67	32.5	27.5	1 ♀, 10 ♂	Underground
	Aug. 27 '72	31.6	30.1	1 ♀, 15 ♂	Underground

The temperature readings were taken in the centre of the nest and in the shade or in the cavity in the vicinity of each nest.

probably attributable to the natural output of heat which is generated as a by-product of metabolism in the colony. According to CHAUVIN (1968) a honeybee generates at least 0.1 calorie per minute at 10°C under most conditions. In *Vespa* colonies, too, a certain amount of heat would presumably be produced by all the members of the colonies. ISHAY and RUTNER (1971) reported in *V. crabro* colonies that the movements of larvae and their metabolic activities could create sufficient heat to maintain reasonable thermoregulation in nests even in the absence of adults, and in pupal cells a constant temperature of ca.30°C was maintained, although diurnal fluctuations in larval cells was much greater.

When the nest temperature reaches some point around 30°C the workers begin to fan with their wings inside the nest. If the temperature continues to rise, more workers engage in such alar ventilation not only inside the nest but on the surface of the envelope, and some workers begin to bring water which is then deposited as droplets on the caps of cocoons of the pupal cells. Other workers suck the droplets of water and then spread it into thin films on the comb surface, extending the tongues outward. As other workers fan with their wings to drive moist air away and out of the nest, the water evaporates and cools the air in the nest. Similar behaviour of both fanning and water droplets to cool overheated nests are reported among the colonies of *Polistes* (STEINER 1930), *Polybia* (SCHWARZ 1931), *Vespula* (WEYRAUCH 1936, GAUL 1952, KEMPER and DÖHRING 1967) and the honeybee (PARK 1925, LINDAUER 1961).

In addition to the ways mentioned above, the regulation of the nest temperature is efficiently accomplished

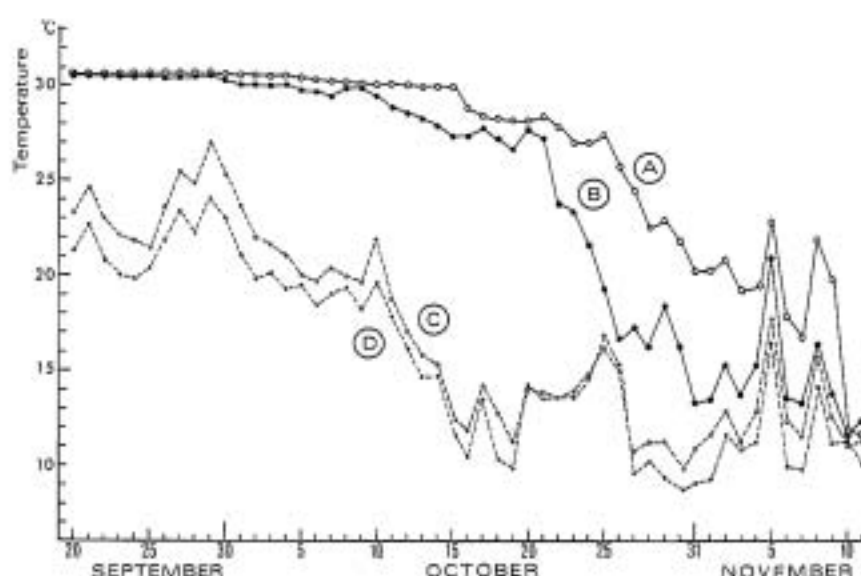


Fig. 28. Fluctuations of the temperature within the nests of *Vespa analis* and *V. simillima* compared with the air outside the nest at 22:30 during autumn, 1969. The number of occupants was ca. 650 workers in *V. simillima* colony and ca. 70 workers in *V. analis* colony, respectively, on September 20th. A: nest temperature of *V. simillima*; B: nest temperature of *V. analis*; C: air temperature in the vespiary; D: air temperature outside the vespiary.

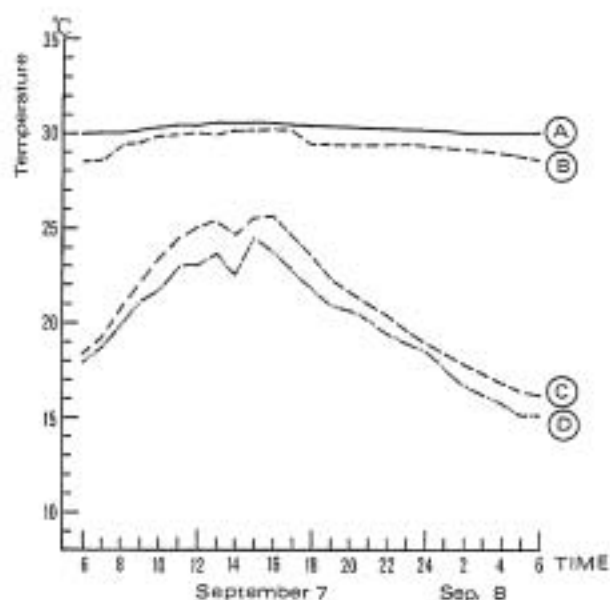


Fig. 29. Diurnal fluctuations of nest temperature in *Vespa simillima* and *V. analis* colonies. The number of occupants was ca. 550 in *V. simillima* and ca. 60 in *V. analis*, respectively. Notation as in Fig. 28.

by adding numerous air spaces in the envelope, sometimes as much as 10cm thick in *V. simillima*, which help to insulate the comb from the influence of external temperature. In *V. orientalis*, ISHAY et al(1971) observed

that the hornets wall off most of the nest entrance and construct "special envelopes" around the populated combs when the nest temperature drops below the optimal point at the end of the season: I have not so far observed such behaviour in the Japanese *Vespa*. The nest temperature, however, decreases along with the drop in air temperature outside because death of workers as well as departure of the sexuals brings about a diminution of the population size in colonies as autumn is far advanced as shown in Fig. 28. A sudden drop in nest temperature of both species, *V. simillima* and *V. analis*, at the end of October seems to have been caused by cessation of activity within the nests.

#### 6. Nest defence and aggressiveness

All *Vespa* species are generally regarded as extremely aggressive and dangerous, but the queens of all the species in Japan are less aggressive than workers. Usually she does not attack man and animals even if the nest is disturbed by them, though she shows great alarm and rushes about on the envelope and comb or flies around the nest. On the other hand, at the invasion by alien queens, frequently observed in *V. crabro* before and after emergence of workers (JANEY 1903), all inhabitants, both queen and workers, rush at the intruder and attack with mandibles and stings to kill it (MATSUURA 1970).

The workers of various species show markedly different reactions with regard to disturbance of their nests. The relative aggressiveness of various species to men and animals at or near their own nests is in the order: *mandarinia* - *simillima* - *crabro* - *analis* - *tropica*. The first three species are soon provoked to attack with regard to an approach to their nest, as is *V. velutina* in Formosa. (MATSUURA 1973). In my experience these workers usually attacked and followed the men who approached the nests within about 5-10m. As soon as a guard at the entrance is alerted by the sight of a large object moving nearby, she may dart suddenly from the entrance to the surface envelope. This causes a general rise in activity and other workers in the nest begin to dart and flip their wings over the envelope. The nest now bristles with aggressive hornets and an audible vibration throughout the entire colony is caused. On the other hand, *V. analis* is not a very aggressive hornet as pointed out by VECHT (1957). Usually the workers of this species do not attack unless the nest is disturbed and one can approach the nest to about 1m without any attack. However, when the nest is disturbed many workers hurry out of the entrance and run in all directions over the envelope. Some of them fly around the nest to carry out an attack. *V. tropica* is the least aggressive of the Japanese hornets: although I observed about 40 nests the workers of this species did not attack me even at the time of collecting the nest without any anaesthetization, though they violently flew around me and threatened me by a particular loud clicking produced by rapid opening and closing of the mandibles. This clicking is produced in all *Vespa* species at or near their nests and is regarded as characteristic of or prevalent in the genus. In *V. mandarinia* it is produced not only at the nest but also at the occupied hives and nests of other social wasps and tree sap sources frequently visited. This indicates it well developed territorial defence. On the other hand, the other four species make the clicking behaviour only at or near their nests.

During the daytime in all Japanese *Vespa* species there are no hornets on the envelope except for the workers engaged in making the envelope and in fanning. In *V. simillima* several tens of workers always stay overnight on the envelope centering around the entrance, unlike the other four species in which the workers are all inside the nest at night. These guard workers on the envelope run in all directions over the envelope and around the nest without any flight as soon as a nest is disturbed in the evening and night. In the other species there are several guards positioned at the nest entrance at night. They hurry out of the entrance to carry out an attack when man or animals approach too closely.

It seems that the defensive power of a colony of *Vespa* is directly related to the size of the population. *V. analis* and *V. tropica* belong to the small population type, never exceeding 1,000 in cell number, being equal or smaller in colony size in comparison with *Polistes* species of the largest colony, such as *P. chinensis*, *P. snelleni* and *P. rothneyi* (MATSUURA 1970). On the other hand, *V. mandarinia*, *V. simillima* and *V. crabro*, regarded as aggressive species, are to be classified in the large population type and exceed 4,000 in maximum cell number as shown in chap. V. Population dynamics.

#### Discussion

*Vespa* extend well into the subtropics and tropics, where predation by ants on nest contents is a serious

threat during the solitary nesting period, especially when the queen is on a foraging trip, as stressed by JEANNE (1975). The queen nests of the flask-shaped type with a cylindrical vestibule built by only twig-nesting species of *V. analis* and *V. affinis*, essentially subtropical or tropical species, could serve as a protection against predators as suggested by YAMANE and MAKINO (1977). A similar structure has been reported in the queen nests of some *Dolichovespula* species, such as *D. maculata* (RAU 1929, DUNCAN 1939, TAKAMIZAWA per. com.) which build essentially aerial nests suspended from tree branches. As the ants are a serious contributor to colony failure in queen nests of some tree nesting *Polistes* in the temperate regions, too (YOSHIKAWA 1957, MIYANO 1980), the long vestibule is regarded as an adaptation for brood defence in vespine nests of tree nesting species.

The nests of the bowl-shaped type are found in the species with a rather southern distribution, such as *V. mandarinia* and *V. tropica*. They build nests exclusively in concealed or underground sites, where this nesting habit may reduce the danger from ant predation, and assist with thermoregulation during the solitary stage. The incomplete covering of the combs in these species could be regarded as adaptations to such nidifications.

On the other hand, the nests of the ball-shaped type are only built by typically temperate species, such as *V. crabro* and *V. simillima* with a rather northern distribution (VEICHT 1959). According to DUNCAN (1939), *V. crabro* builds an envelope if the nest is made in the open but not if made in hollow trees, except perhaps a few rudiments above the first comb, and subterranean nests usually have envelopes except for those built in very hard and stony ground in which the stones prevent normal expansion of the nest. JANET (1885) reported an aerial queen nest of *V. crabro* with two envelope sheets. These facts show that this species has the ability to change the type of envelope according to its nest site environment, though *V. crabro flavofasciata* in Japan always builds a spherical envelope either in a subterranean or in an aerial nest. The many complete envelopes in queen nests is more advantageous as a protection for extreme temperature fluctuations in temperate regions. In this respect the many-sheeted envelope of *V. simillima*, as well as that of *Vespa* and *Dolichovespula*, is considered principally an adaptive feature against cold spring weather. It serves to trap air in spaces to greatly minimize heat loss during the solitary period when only the queen and a few mature larvae produce heat (ISHAY 1973, GIBO 1977).

In these two species another dramatic strategy in nesting habits is the adoption of the relocation of nests. The queens of both species build primarily in small spaces or narrow cavities where the microclimate is most suitable for the early stages of development, as the ability of the colony to regulate to nest temperature is severely limited. When the nest becomes too large, the whole colony moves to a new, more spacious site, because the colony is then able to regulate the temperature within the nest. Thus, this habit also appears to be an adaptation to cold weather by producing workers as rapidly as possible.

Thermoregulation should be much easier for mature colonies than for the younger ones of the vespine wasps because the temperature inside the nest is effectively controlled, as the combs are surrounded by numerous small air pockets with the increase in numbers of envelopes covering the combs. This ability to thermoregulate enabled the vespine wasps in temperate regions to make better use of the longer season of favourable weather for the development of the colony and the high, relatively constant temperature of mature colonies can play a vital part in queen production in the cool autumn season. Compared to the vespine wasps, polistine wasps, which build a nest without an envelope a much shorter life cycle in which to rear the sexuals during the hot summer season (YOSHIKAWA 1962, WEST-EBERHARD 1969, YAMANE 1969, MATSUURA 1980) because the colonies are unable to insulate themselves against unfavourable autumn weather. Thus, the prolonged life cycle of the vespine wasps in temperate zones is compensated by not only producing more queens and males, but also building up more populous colonies which evolve defenses against predators.

### III. FEEDING HABITS

The food of hornets consists of two well defined classes, liquids and solids. The former is carbohydrate food consumed mainly by adult hornets, while the latter is protein food eaten entirely by larvae. These substances are obtained by the hornets from many different sources, and they have evolved various strategies of finding them.

This chapter describes the feeding habits of *Vespa* and some specific differences in the mode of food



collection among them.

1. Food sources

1) Carbohydrates

Carbohydrates are obtained from tree sap, honeydew of aphids and psyllids, flower nectar and other sources as listed in Table 12. The most important carbohydrate source for all the *Vespa* species is the tree sap exuding from living trees, especially *Quercus* spp. (Fig. 30). The relative frequency of visits to tree sap



Fig. 30. Uninseminated queen(top), and workers(centre) of *Vespa mandarinia*, and queens of *Vespa tropica* (right and bottom), visiting tree sap.

sources by various *Vespa* species is in the following order: *mandarinia* > *crabro* > *anis* > *tropica* > *simillima*. The tree aperture exuding sap is usually occupied by *V. mandarinia*, which claim the territorial right by chasing all the visitors of same or different species of hornets, beetles, butterflies, flies and other insects from the place where the secretion is abundant. Both intra- and interspecifically a distinct linear dominance order is recognized among the hornets visiting tree sap and two or more species cannot settle at one tree aperture at the same time as discussed later.

Flower nectar is gathered from eight species of five families of flowering plants like *Camellia* spp., *Cayratia japonica* (Fig. 31), *Mahonia fortunei*, etc., in which the nectaries are well exposed and the flowers have rather abundant nectaries. It seems likely that *Vespa* do not rely extensively on flower nectar, because

Table 12. Carbohydrate sources of *Vespa* species (1)

Sources	Species*	<i>Vespa</i> species**				
		Sim	Cra	Ana	Man	Tro
Tree sap	Fam. Salicaceae					
	1. <i>Salix gracilistyla</i> MIO.	○	○	○	○	○
	Fam. Fagaceae					
	2. <i>Quercus serrata</i> THUNB.	○	○	○	○	○
	3. <i>Q. acutissima</i> CARRATH.	○	○	○	○	○
	4. <i>Q. glauca</i> THUNB.	○	○	○	○	○
	5. <i>Shiia cuspidata</i> MAKINO	○	○	○	○	○
	Fam. Ulmaceae					
	6. <i>Ulmus parvifolia</i> JACQ.	○	○	○	○	○
	7. <i>Setkova serrata</i> MAKINO	○	○			
Flower nectar	Fam. Rutaceae					
	8. <i>Citrus unshiu</i> MARCOV.	○			○	
	Fam. Euphorbiaceae					
	9. <i>Mallotus japonicus</i> MUEL. ARG.	○				
	Fam. Berberidaceae					
	10. <i>Mahonia fortunei</i> FEDDE	○		○		
	Fam. Vitaceae					
	11. <i>Cayratia japonica</i> GAGN.		○	○	○	○
	12. <i>Ampelopsis brevipedunculata</i> TRANTV.	○	○		○	○
	Fam. Theaceae					
Ripe fruit	13. <i>Camellia japonica</i> L.	○				
	14. <i>C. sasanqua</i> THUNB.	○		○	○	
	Fam. Umbelliferae					
	15. <i>Foeniculum vulgare</i> MILL.					○
	16. <i>Angelica polyclada</i> FRANCH.	○	○	○		
	Fam. Gentianaceae					
	17. <i>Gentiana scabra</i> BUNGE	○				
	Fam. Moraceae					
	18. <i>Ficus carica</i> L.	○	○	○	○	○
	Fam. Anonaceae					
Ripe fruit	19. <i>Asimina triloba</i> DUAL	○			○	○
	Fam. Rosaceae					
	20. <i>Prunus persica</i> BATSCH.		○		○	○
	21. <i>Pyrus serotina</i> REIDER	○		○	○	○
	Fam. Vitaceae					
	22. <i>Vitis vinifera</i> L.	○			○	○
	Fam. Ebenaceae					
	23. <i>Diospyros kaki</i> THUNB.	○		○	○	○
	Fam. Solanaceae					
	24. <i>Lycopersicon esculentum</i> MILL.		○		○	
Ripe fruit	Fam. Cucurbitaceae					
	25. <i>Citrullus battich</i> FORSKAL.	○				
Ripe fruit	Fam. Bromeliaceae					
	26. <i>Ananas comosus</i> MERR.				○	

Table 12. continued (2)

Sources	Species*	Vespa species**				
		Sim	Cra	Ana	Man	Tro
Honeydew	Insecta					
	Fam. Coccidae					
	27. <i>Ceroplastes rubens</i> MASKELL			o		
	Fam. Psyllidae					
	28. <i>Psylla tobinae</i> MEYATAKE			o		
	Fam. Aphididae					
	29. <i>Lachnus tropicalis</i> GOOT			o		
	30. <i>Toxoptera citricidus</i> KIRKALDY	o		o		
	31. <i>T. odinae</i> GOOT			o		
Mushroom	Gasteromycetes					
	Hymenogasterales					
	32. <i>Kobayasia nipponica</i> IMAI et KAWAM.			o	o	o
Manufactured sweets	33. Syrup juice	o	o	o	o	o

\* Scientific names of plant species from MAKINO's new illustrated flora of Japan by MAKINO, HARA and TSUYAMA 1961.

\*\* Sim: *V. similima*, Cra: *V. crabro*, Ana: *V. analis*, Man: *V. mandarinia*, Tro: *V. tropica*.



Fig. 31. *Vespa similima* worker taking nectar from the flowers of *Cayratia japonica*.



Fig. 32. *Vespa mandarinia* worker feeding on a fig.

they have a broad head and short tongue and probably because the amount of nectar collected per flower is so small that it does not suffice for their nutritional requirements.

The juices of well-ripened fruits are also consumed in great quantities whenever available. Figs are especially preferred by workers of most *Vespa* species during late summer and autumn (Fig. 32). The attack usually occurs when the fruits are ripe on the tree and just enough for picking. The workers of *V. mandarinia* frequently chew and suck the tissues en masse and cause serious damage and loss to the fruit grower. Workers of *V. tropica* also suck the juices from over-ripe fruits of peaches, pears and persimmons attached to the tree. In case of grapes, tomatoes, pineapples and water melons, I have observed some *Vespa* workers feeding on dropped or discarded ones on the ground in the orchards.

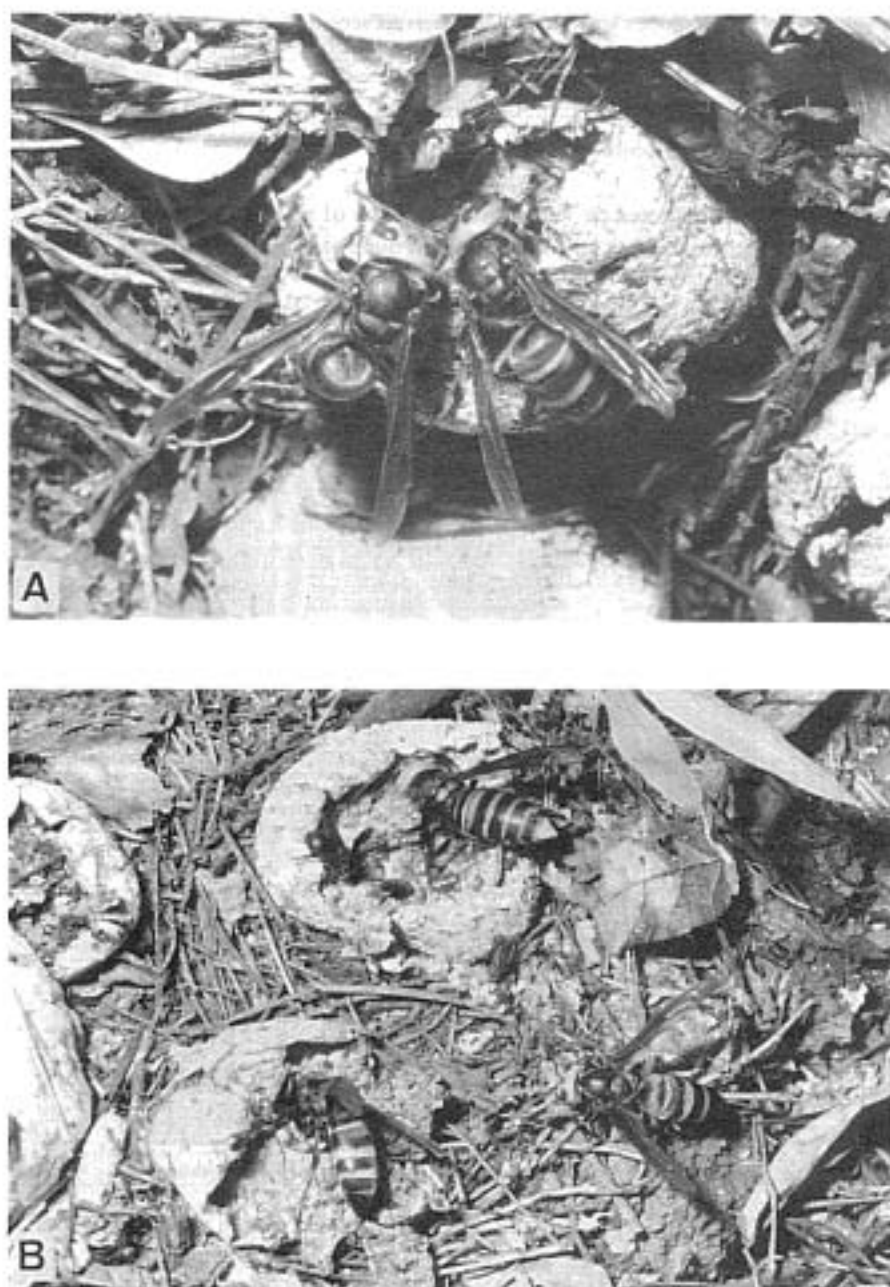


Fig. 33. *Vespa* workers feeding on mushrooms: A, *V. analis*; B, *V. mandarinia* (top) and *V. tropica* (bottom).

The mushroom is an unusually source of carbohydrate for vespine wasps. However, workers of most *Vespa* species make it a regular part of their diet in autumn (Fig. 33). Furthermore, males of *V. mandarinia* appear to be most attracted and take it as their principal food source after leaving their nest. I have never observed them feeding on any other foods in the field.

Honeydew produced by aphids, scale insects and jumping plant lice, was collected from leaves by only

*V. analis*, while other *Vespa* species scarcely visited the sweet secretion, though it is well-known that *Vespula* and *Dolichovespula* species frequently collect it as a rich source of carbohydrate (DUNCAN 1939, EDWARDS 1980).

Syrup juice was collected whenever available by most *Vespa* species, which have been observed licking it at a pile of empty tins and bottles.

## 2) Protein

Most of the protein food collected by *Vespa* species consists of insects and spiders as listed in Table 13. Judging from these records, though still insufficient in numbers observed, it seems that prey preference of *Vespa* differs characteristically with species.

*V. simillima* tends to hunt a wide range of insects and spiders (Figs. 34 and 35). More than 44 species of winged insect from 8 different orders and several species of spiders were observed as its prey. Of these, flies of the following families are particularly preferred: Tabanidae, Syrphidae, Muscidae, Anthomyiidae



Fig. 34. *Vespa simillima* worker hunting a long-horned grasshopper.

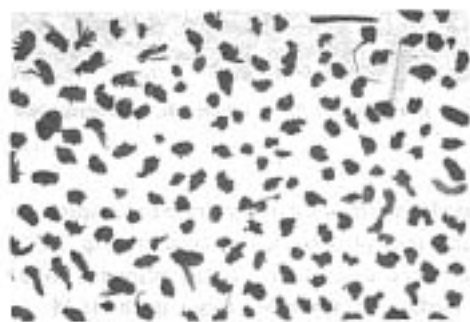


Fig. 35. Prey loads brought back to the nest by *Vespa simillima* workers.



Table 13. Prey of *Vespa* species (1)

Prey species	Stage of prey*	Frequency of obser.
<i>V. similima</i>		
Insecta		
Orthoptera		
Fam. Locustidae		
1. <i>Parapodisma mikado</i> BOLIVAR	L.A	6
2. <i>Atractomorpha bedeli</i> BOLIVAR	A	12
Fam. Tettigoniidae		
3. <i>Phaneroptera fakata</i> PODA	L.A	9
4. <i>P. sp.</i>	L.A	8
Mantodea		
Fam. Mantidae		
5. <i>Paratenodera aridifolia</i> STOLL	L.A	5
6. <i>Gn. sp.</i>	L.A	12
Odonata		
Fam. Libellulidae		
7. <i>Orthetrum triangulare</i> SELYS	A	2
8. <i>Sympetrum frequens</i> SELYS	A	45
9. <i>Gn. spp.</i>	A	31
Hemiptera		
Fam. Cicadidae		
10. <i>Graptopsaltria nigrafuscata</i> MOTSCHULSKY	A	3
11. <i>Platypleura kaempferi</i> FABRICIUS	A	102
12. <i>Meimuna opalifera</i> WALKER	A	25
Lepidoptera		
Fam. Noctuidae		
13. <i>Gn. spp.</i>	L.A	38
Fam. Nymphalidae		
14. <i>Vanessa indica</i> HERBST	A	2
Coleoptera		
Fam. Scarabaeidae		
15. <i>Popillia japonica</i> NEWMAN	A	25
Fam. Chrysomellidae		
16. <i>Gn. spp.</i>	A	8
Fam. Attelabidae		
17. <i>Macorhis ursulus</i> ROELOFS	A	1
Hymenoptera		
Fam. Vespidae		
18. <i>Eumenes spp.</i>	A	11
19. <i>Vespula flaviceps</i> SMITH	A	14
Fam. Apidae		
20. <i>Apis mellifera</i> L.	A	>100
21. <i>A. cerana</i> FABRICIUS	A	24
Diptera		
Fam. Stratiomyidae		
22. <i>Plecticus aurifer</i> WALKER	A	34
23. <i>Hermetia illucens</i> L.	A	15

Table 13. continued (2)

Prey species	Stage of prey*	Frequency of obser.
Fam. Tabanidae		
24. Gn. spp.	A	67
Fam. Asilidae		
25. <i>Chorades</i> sp.	A	34
Fam. Bombyliidae		
26. Gn. spp.	A	26
Fam. Syrphidae		
27. <i>Chrysotoxum</i> spp.	A	32
28. <i>Eristalis cerealis</i> FABRICIUS	A	18
29. <i>Lathyrrophthalmus</i> sp.	A	7
30. <i>Eristalomyia tenax</i> L.	A	88
31. <i>Megaspis zonata</i> FABRICIUS	A	6
32. <i>Eumerus</i> spp.	A	32
33. <i>Epistrophe balteata</i> de GEER	A	7
34. <i>Syrphus</i> spp.	A	43
Fam. Muscidae		
35. <i>Muscina</i> spp.	A	95
36. Gn. spp.	A	87
Fam. Anthomyiidae		
37. <i>Polletes lardaria</i> FABRICIUS	A	15
38. Gn. spp.	A	38
Fam. Calliphoridae		
39. <i>Calliphora lata</i> COQUILLET	A	41
40. <i>Lucilia caesar</i> L.	A	19
41. Gn. spp.	A	54
Fam. Sarcophagidae		
42. <i>Boettcherisca</i> sp.	A	28
Fam. Scatophagidae		
43. <i>Scathophaga stercorarium</i> L.	A	12
Arachnida		
Araneae		
44. Gn. spp.	A	55
<i>V. analis</i>		
Insecta		
Orthoptera		
Fam. Locustidae		
1. <i>Atractomorpha bedeli</i> BOLIVER	L	3
Mantodea		
Fam. Mantidae		
2. <i>Paratenodera aridifolia</i> STOLL	L.A	18
3. <i>Acromantis japonica</i> WESTWOOD	A	15
Odonata		
Fam. Libellulidae		
4. <i>Sympetrum frequens</i> SELYS	A	25

Table 13. continued (3)

Prey species	Stage of prey*	Frequency of obser.
<b>Hemiptera</b>		
Fam. Cicadidae		
5. <i>Melmuna opallifera</i> WALKER	A	19
Fam. Coreidae		
6. <i>Riptortus clavatus</i> THUNBERG	A	2
7. Gn. spp.	A	4
<b>Lepidoptera</b>		
Fam. Sphingidae		
8. <i>Sphinx ligustri</i> BUTLER	L	1
Fam. Noctuidae		
9. Gn. spp.	L	33
<b>Coleoptera</b>		
Fam. Harpalidae		
10. <i>Chlaenius</i> sp.	A	2
11. Gn. spp.	A	3
Fam. Scarabaeidae		
12. Gn. spp.	A	18
Fam. Tenebrionidae		
13. <i>Plesiophthalmus nigrocyaneus</i> MOTSCHULSKY	A	3
<b>Hymenoptera</b>		
Fam. Tiphidae		
14. <i>Tiphia</i> spp.	A	5
Fam. Colletidae		
15. <i>Colletes</i> spp.	A	5
Fam. Andrenidae		
16. <i>Andrena</i> spp.	A	7
Fam. Halictidae		
17. <i>Halictus</i> spp.	A	8
18. <i>Lasioglossum</i> spp.	A	9
Fam. Megachilidae		
19. <i>Megachile xanthothrix</i> YASUMATSU et HIRASHIMA	A	3
20. <i>M. tsurugensis</i> COCKRELL	A	2
21. <i>M.</i> spp.	A	5
Fam. Apidae		
22. <i>Tetralonia</i> sp.	A	3
23. <i>Apis mellifera</i> L.	A	33
24. <i>A. cerana</i> FABRICIUS	A	12
Fam. Sphecidae		
25. <i>Larra amplipennis</i> SMITH	A	2
26. <i>Sceliphron inflexum</i> SICKMANN	A	1
27. <i>Cerceris</i> spp.	A	3
Fam. Vespidae		
28. <i>Eumenes</i> spp.	A	7
29. <i>Orancistrocerus drewseni</i> SAUSSURE	A	5
30. <i>Polistes snelleni</i> SAUSSURE	A	2

Table 13. continued (4)

Prey species	Stage of prey*	Frequency of obser.
31. <i>P. japonicus</i> SAUSSURE	A	3
32. <i>P. mandarinus</i> SAUSSURE	A	3
33. <i>P. jadvigae</i> DALLA TORRE	A	20
34. <i>P. chinensis</i> FABRICIUS	A	17
35. <i>Parapolybia indica</i> SAUSSURE	A	6
36. <i>Vespa similis</i> SMITH	A	3
37. <i>Vespula flaviceps</i> SMITH	A	23
Diptera		
Fam. Stratiomyidae		
38. <i>Plecticus aurifer</i> WALKER	A	45
39. <i>Hermetia illucens</i> L.	A	26
Fam. Asilidae		
40. <i>Chorodactylus</i> sp.	A	13
41. Gn. sp.	A	15
Fam. Syrphidae		
42. <i>Eristalomyia tenax</i> L.	A	18
43. <i>Syrphus</i> spp.	A	12
44. Gn. spp.	A	19
Fam. Muscidae		
45. <i>Musca</i> spp.	A	23
46. Gn. spp.	A	10
Fam. Calliphoridae		
47. <i>Calliphora lata</i> COQUILLET	A	9
48. <i>Lucilia caesar</i> L.	A	4
49. Gn. spp.	A	18
Fam. Sarcophagidae		
50. <i>Boettcherisca</i> sp.	A	3
51. Gn. sp.	A	3
Fam. Scatophagidae		
52. <i>Scathophaga stercorarium</i> L.	A	2
Arachnida		
Araneae		
53. Gn. spp.	L.A	28
<i>V. crabro</i>		
Insecta		
Orthoptera		
Fam. Tettigoniidae		
1. <i>Holochlora</i> sp.	A	3
Odonata		
Fam. Gomphidae		
2. <i>Sieboldius albardae</i> Selys	A	1
Hemiptera		
Fam. Cicadidae		
3. <i>Cryptotympana japonensis</i> KATO	A	145
4. <i>Graptopsaltria nigrofusca</i> MOTSCHULSKY	A	34

Table 13. continued (5)

Prey species	Stage of prey*	Frequency of obser.
5. <i>Platypleura kaempferi</i> FABRICIUS	A	107
6. <i>Meimuna opalifera</i> WALKER	A	88
Hymenoptera		
Fam. Vespidae		
7. <i>Polistes mandarinus</i> SAUSSURE	A	4
Fam. Apidae		
8. <i>Apis mellifera</i> L.	A	10
<i>V. mandarinia</i>		
Insecta		
Mantodea		
Fam. Mantidae		
1. <i>Paratenodera aridifolia</i> STOLL	LA	12
2. <i>Hierodula patellifera</i> SERVILE	LA	9
3. Gn. spp.	A	6
Lepidoptera		
Fam. Papilionidae		
4. <i>Papilio xuthus</i> L.	L	13
Fam. Sphingidae		
5. Gn. spp.	L	18
Coleoptera		
Fam. Scarabaeidae		
6. <i>Anomala cuprea</i> HOPE	A	107
7. <i>A. albopilosa</i> HOPE	A	15
8. <i>A.</i> spp.	A	132
9. <i>Mimela splendens</i> GYLLENHAL	A	54
10. <i>Mimela</i> spp.	A	32
11. <i>Lachnosterna</i> spp.	A	24
Hymenoptera		
Fam. Apidae		
12. <i>Apis mellifera</i> L.	L.P.A	140
13. <i>A. cerana</i> FABRICIUS	L.P.A	50
Fam. Vespidae		
14. <i>Polistes mandarinus</i> SAUSSURE	L.P.A	22
15. <i>P. jadwigae</i> DALLA TORRE	L.P.A	54
16. <i>P. rothneyi</i> CAMERON	L.P.A	27
17. <i>Vespa similima</i> SMITH	L.P.A	352
18. <i>V. crabro</i> L.	L.P.A	38
19. <i>V. analis</i> FABRICIUS	L.P.A	129
20. <i>V. tropica</i> L.	L.P.A	11
21. <i>Vespula flaviceps</i> SMITH	L.P.A	178
Arachnida		
Araneae		
Fam. Argiopidae		
22. <i>Argiope amoena</i> AUDOUIN	LA	38



Table 13. continued (6)

Prey species	Stage of prey*	Frequency of obser.
23. <i>A. bruennichii</i> SCOPOLI	L.A	25
<i>V. tropica</i>		
Insecta		
Hymenoptera		
Fam. Vespidae		
1. <i>Polistes snelleni</i> SAUSSURE	L.P	20
2. <i>P. japonicus</i> SAUSSURE	L.P	26
3. <i>P. mandarinus</i> SAUSSURE	L.P	12
4. <i>P. jodwigae</i> DALLA TORRE	L.P	358
5. <i>P. rothneyi</i> CAMERON	L.P	34
6. <i>P. chinensis</i> FABRICIUS	L.P	54
7. <i>Parapolybia indica</i> SAUSSURE	L.P	42
8. <i>P. sp.</i>	L.P	23

\* L; larva, P; pupa, A; adult.



Fig. 36. *Vespa analis* worker hunting a cicada, *Meimuna opalifera*.

and Calliphoridae. This hornet is able to catch such active insects owing to its very swift and agile movements. A few larvae of any insect have been observed to be collected by this species, though many soft-bodied insects, which were converted to meat pellets, were sometimes carried into the nest.

*V. analis* also tends to take various insects (Fig. 36). More than 53 species of insects from 8 orders were observed, together with some immatures of mantids and sphinx moths. The most important prey were adults of various species of Hymenoptera such as polistine wasps and bees. The workers of this hornet, with its agile flight activity, hunt particularly for such active insects visiting flowers.

Compared to other *Vespa* species, information on prey of *V. crabro* are not sufficient for conclusions. Only 8 species of insects from 4 orders were observed and the dominant prey were adults of various cicadas. As already reported by DAVIS (1925) this species is very skillful in capturing a cicada and the workers attack



Fig. 37. *Vespa crabro* worker hunting a cicada, *Graptopsaltria nigrofuscata*.



Fig. 38. *Vespa crabro* workers handling a pellet of a cicada brought in the nest.



Fig. 39. *Vespa tropica* queen attacking a *Polistes jadwigae* nest.



Fig. 40. Hunting of *Vespa mandarinia*: A, worker attacking a beetle of *Anomala cuprea*; B, worker cutting up the mantid, *Hierodula patellifera*.

4 species of cicada in and near Kibi. One of the most preferred cicadas is *Cryptotympana facialis*, which is the largest in body size of the Japanese cicadas (Figs. 37 and 38). I frequently observed that several of the cicadas were taken one after another when very abundant and when their capture was easy. One observation on colony C7303 with about 120 workers showed that 37 loads of only this large cicada, which was estimated to correspond to at least 12 individuals of the adult cicada which had been brought to the nest by 5 marked workers within three hours on August 10th, 1973. In another nest (C6802) with about 240 workers the loads of the cicada occupied as much as 71.6% of the 74 loads examined at the nest entrance on August 6th, 1968.

*V. tropica* depends almost exclusively on the brood of Polistinae wasps for its protein food (Fig. 39). I have never seen this hornet attacking any other species of arthropod. All 8 species of polistinae wasps occurring in and near Kibi were attacked by both queen and worker hornets of this species. A detailed account is given in the following section.

*V. mandarinia* is not very skillful at capturing agile insects. Both queen and worker hornets of this species hunt large caterpillars and beetles (Fig. 40) as listed in Table 13. But the most remarkable trait of this hornet is the hunting of other social wasps and honeybees, attacking and often exterminating their

colonies. These habits are quite different from those of other *Vespa* species and the peculiarities are described later in this chapter.

## 2. Food dependence of *Vespa tropica* on polistine wasps

*Vespa tropica* depends on various polistine wasps for its protein food. Though the habit of attacking the lesser social vespids is reported by many observers (*Ropalidia*; RUITTER 1916, *Stenogaster*; WILLIAMS 1919, WARD 1965, *Polistes*; SONAN 1927, 1951, SAKAGAMI and FUKUSHIMA 1957, *Parapolybia*; VECHT 1957, SEKIJIMA et al. 1981), these previous descriptions are mostly fragmentary or superficial, and the specific character of this species is not well-known in detail. This section deals with the habit, which is quite different from that of other congeneric species.

### 1) Collection of prey

When *V. tropica* attacks an active nest of *Polistes* wasps the majority of *Polistes* workers escape to places near the nest such as eaves of buildings or twigs, leaving the queen and a few workers on the comb with no sign of resistance. The hornet pays little attention to some workers still sitting on the comb and opens first a cocoon with its mandibles pulling out the prepupa or young whitish pupa. She holds on to the comb with the two hind pairs of legs, keeping the prey in the fore legs and mandibles. Then, she begins to malaxate it thoroughly, turning it counter-clockwise with the fore legs. Simultaneously she sucks fluid from the prey and stores it in her crop. After the contents are swallowed, the victim is made into a small ball composed of unconsumed remnants and is thrown to the ground under the nest. In the case of large *Polistes* species such as *P. jadvigae* and *P. rothneyi*, a single prepupa provides enough fluid to be carried away, but in smaller species such as *P. snelleni* and *P. chinensis*, the contents of two or three individuals are successively swallowed. The duration spent in chewing was 130–250 sec. ( $\bar{m}=185.0$ ,  $n=72$ ).

The prey were transported as fluid in 340 observations except for only two instances in which the hornet transported the food into the nest between its mandibles as a single fresh ball in a similar manner to that of other *Vespa* species.

The *Polistes* adults having escaped from the attacked nest return after the hornet flies away, though the nest once found by the hornet is continuously visited by the individual for several days (Table 16 and Fig. 42). After all the prepupae are taken, the hornets shift to the full grown larvae or older pupae and finally to later stage pupae and immature larvae. However, I have never observed the hornet catch any *Polistes* adults.

Occasionally, alien hornets appear near the nest during the chewing, but they are chased away by the "owners" with or without combat. In all cases so far observed ( $>400$ ), *Polistes* nests were always attacked and occupied by a single hornet, though SAKAGAMI and FUKUSHIMA (1957) state that the hornet worker often comes back accompanied with one or two nestmates after the first visit.

### 2) Phenology of visits to *Polistes* colonies

Overwintered queens of *Polistes* wasps begin to establish their nests in early-middle April in and near Kibi. In *Polistes jadvigae*, the most populous species in the area, the days of the first foundation of their nest were: April 10th (1967), 15th ('68), 13th ('69), 15th ('70), 2nd ('71), 7th ('73), 13th ('74) and 13th ('75). Thereafter, development of the *P. jadvigae* colony proceeds generally in the following seasonal pattern (Fig. 41): (1) Emergence of first workers - early June, (2) Reproduction of males and new queens - mid-July to late August, (3) Maximum development of brood population - late July to early August, (4) Rapid cessation of brood rearing - late August, and (5) Disintegration - mid- to late September. On the other hand, *V. tropica* queens commence to build their nests in late May to early June (Fig. 2), about two months later than *Polistes* species, just when the first few workers of *Polistes* wasps begin to emerge in the colony.

The first attacks by *V. tropica* queens on *Polistes* colonies are observed from early to mid-June (Table 14). Visits become constant, thereafter, with the colony development throughout the solitary nesting period. After the emergence of *V. tropica* workers in mid- to late July (Table 3 and Fig. 41), the queen still continues foraging activities until late July to mid-August, then ceases to attack *Polistes* colonies. On the

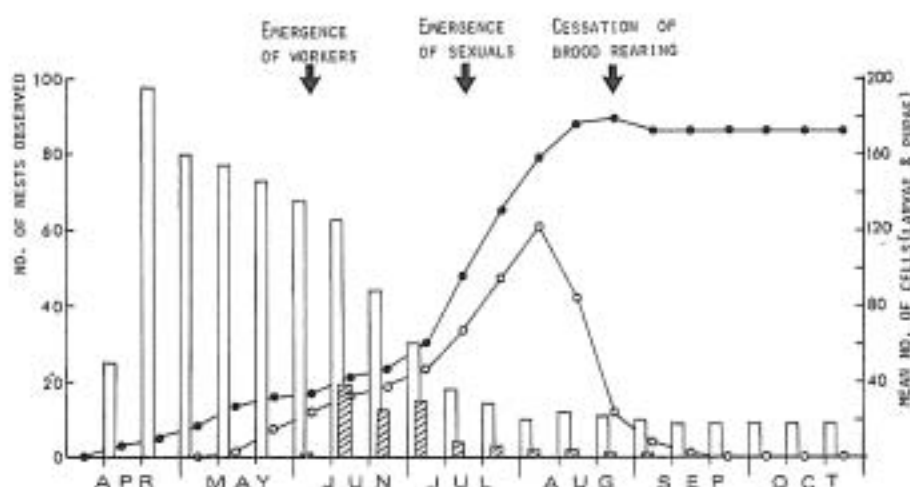


Fig. 41. Seasonal changes in the number of active nests of *Polistes jadwigae* (open areas) and those of the nests attacked by *Vespa tropica* (hatched areas) in the Wakayama Fruit Tree Experimental St. field at Kibi in 1971. Solid circles; the mean number of cells in *Polistes jadwigae* colonies; Open circles; the mean number of larvae and pupae in the colonies of *P. jadwigae*.

Table 14. Records of the first and final attack by *Vespa tropica* on pollistine colonies in and near Kibi, 1966-1975.

		Year										Average
		'66	'67	'68	'69	'70	'71	'72	'73	'74	'75	
By <i>V. tropica</i> queens	First attack	Jun.10	Jun. 2	Jun. 1	Jun. 4	Jun.11	Jun. 3	Jun. 2	Jun. 5	Jun. 3	Jun. 6	Jun.4.7
	Final attack	?	Jul.30	?	Aug. 2	Jul.22	Aug.16	?	Jul.18	Aug. 5	Jul.25	Jul.30.1
By <i>V. tropica</i> workers	First attack	Jul.24	Jul.20	Jul.25	Jul.15	Jul.25	Jul.25	Jul.23	Jul.26	Jul.20	Jul.22	Jul.22.5
	Final attack	?	Aug.24	Aug.28	Aug.25	?	Sep. 7	Sep. 2	Aug.26	Aug.28	Aug.25	Aug.28.4

other hand, workers of *V. tropica* begin to visit the nests from late July and continue to attack them until late August to early September (Table 14 and Fig. 41). In *V. tropica* colonies males and new queens are reared from early July and emerge in late August to mid-September and the rearing of the larvae ordinarily ceases in mid- to late August (Fig. 77) in parallel with the completion of brood rearing in *Polistes* colonies (Fig. 41). At the time of emergence of the sexuals foraging activity of workers changes from protein food to carbohydrates such as tree sap and fruit juices. The workers discontinue the rearing of the remaining larvae before the dearth of protein food sources. So they make no more visits to the pollistine nests after mid-September and stop feeding the larvae in the nest. Thus it is clear that the life cycle of *V. tropica* is synchronized with that of pollistine wasps, the principal food source.

### 3) Ratio of *Polistes jadwigae* colonies attacked by *V. tropica*

Table 15 shows the number of *P. jadwigae* nests attacked by *V. tropica*, and the period in which they were destroyed within the confines of the farmstead of Wakayama Fruit Tree Experimental Station over ca.30 hectare area, 1969-1975. The number of nests observed during the time from nest founding to first emergence of workers was 246, of which only one nest was attacked during the seven-year period. After worker emergence the number of nests attacked increased markedly, though the attacked ratio was rather variable for year and period. It ranged from 10.9% in 1970 to 93.2% in 1973 during the period from emergence of first workers to first emergence of sexuals, and 12.5% in 1970 to 80.0% in 1971 during the

Table 15. Number and phase of *Polistes jadwigae* nests attacked by *Vespa tropica* within the confines of the Wakayama Fruit Tree Exp. St., 1969-1975.

Year	Period*			Total no. nests through periods I-III attacked/observed (%)	No. nests** of <i>V. tropica</i>
	I	II	III		
	No. nests attacked /observed (%)	No. nests attacked /observed (%)	No. nests attacked /observed (%)		
1969	0/25 (0)	4/13 (30.8)	13/17 (76.5)	17/45 (37.8)	4
1970	0/27 (0)	5/46 (10.9)	2/16 (12.5)	7/58 (12.1)	1
1971	0/88 (0)	8/38 (21.1)	12/15 (80.0)	20/121 (16.5)	5
1972	0/18 (0)	16/31 (51.6)	9/34 (26.5)	25/47 (53.2)	2
1973	1/48 (2.1)	41/44 (93.2)	3/9 (33.3)	45/58 (77.6)	4
1974	0/22 (0)	9/14 (64.3)	7/12 (58.3)	16/39 (41.0)	2
1975	0/18 (0)	7/12 (58.3)	7/10 (70.0)	14/30 (46.7)	3
Total	1/246 (0.4)	90/198 (45.5)	53/113 (46.9)	144/398 (36.2)	21

\* I: before the emergence of first workers, II: thereafter till the emergence of sexuals, III: thereafter till disintegration.

\*\* Nests discovered within about 500m from the Wakayama Fruit Tree Exp. St..

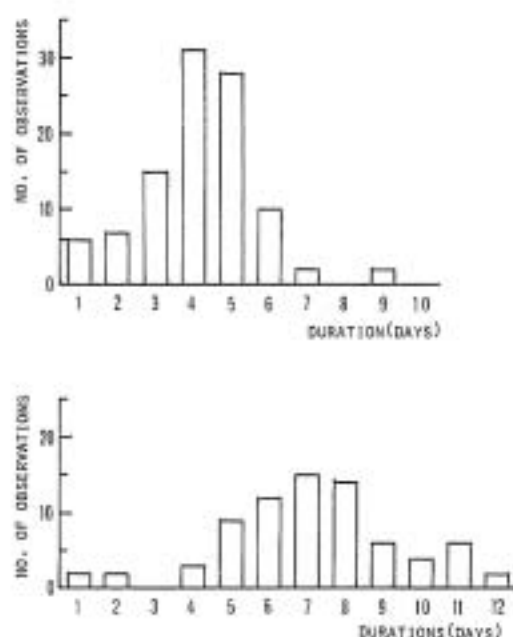
Fig. 42. Predation period of *Vespa tropica* on one nest of *Polistes jadwigae* by a queen (upper) and a worker (lower), 1969-1975.



Table 16. Some records of attack by queens and workers of *Vespa tropica* on *Polistes jadwigae* nests in 1973.

Nest code of <i>P. jadwigae</i>	No. of cells*	<i>V. tropica</i> No.**	Date of		Duration of attack (in days)	Total no. of brood eaten by <i>V. t.</i> ***	No. of brood eaten/day
			first attack	final attack			
Pj 3007	27	Q 00	Jun. 9	Jun. 13	5	12	2.4
Pj 3012	28	Q 00	Jun. 13	Jun. 16	4	9	2.3
Pj 3015	31	Q 00	Jun. 17	Jun. 20	4	14	3.5
Pj 3017	32	Q 00	Jun. 18	Jun. 21	4	13	3.3
Pj 3019	28	Q 00	Jun. 25	Jun. 27	3	10	3.3
Pj 3026	30	Q 02	Jun. 6	Jun. 10	5	11	2.2
Pj 3027	36	Q 02	Jun. 22	Jun. 25	4	16	4.0
Pj 3028	52	Q 03	Jun. 26	Jun. 29	4	18	4.5
Pj 3035	159	W 01	Jul. 27	Aug. 2	7	71	10.1
Pj 3041	207	W 02	Jul. 29	Aug. 4	7	93	13.3
Pj 3047	142	W 03	Aug. 2	Aug. 7	6	53	8.8

\* the number of cells in *P. jadwigae* nest on the day when the first attack by *V. tropica* was observed.

\*\* Q: queen hornet, W: worker hornet.

\*\*\* The number excluding those of eggs and I-III instar larvae.

period after emergence of sexuals. Judging from Tables 14, 15 and Fig. 41, together with other observations, it seems likely that attack before emergence of *Polistes* workers is only performed by *V. tropica* queens and those after emergence of the sexuals are done by the workers largely in late July to mid-August when the development of brood in the *Polistes* colonies reaches a peak.

On the other hand, the number of *V. tropica* nests discovered within about 500m from the Experimental Station varied from one in 1970 to five in 1971 during the seven-year period (Table 15). In 1970 the attacked ratio was remarkably low in the comparison to those in the other six years, either before or after emergence of sexuals in the *Polistes* colonies. This may be due to a low density of *V. tropica* around the survey area in this year.

#### 4) Predation period on a *Polistes* nest

Once a *V. tropica* find a *Polistes* nest she visits the same nest daily until all the brood available are exhausted. Queens of *V. tropica* consecutively attacked a nest of *P. jadwigae* for 1-9 days with an average of 4.5 days (s.d.  $\pm 1.6$ ,  $n=101$ ), and the workers took 1-12 days with an average of 7.2 days (s.d.  $\pm 2.4$ ,  $n=75$ ) to prey upon a colony (Fig. 42). The difference between predation periods of queens and of workers is probably due to the difference in colony size of *P. jadwigae* at the time when they are attacked by *V. tropica*. The attack by *V. tropica* queens takes place mainly on the colony at the period of slow increase with a small number of brood available for prey (Fig. 41), but workers preyed upon 8.8-13.3 immatures per day in late July to early August (Table 16), because more food is then required to maintain their colony as it becomes larger.

#### 5) Fate of attacked colony of *Polistes*

As the attack of *V. tropica* is repeated until all the immature stages are consumed, the nests usually could not recover. When a *Polistes* nest is attacked before emergence of sexuals, the adult wasps finally abandon their original nest, and 89.1% of nests attacked at the period between emergence of workers to that of sexuals were reconstructed by the workers near the original nest (Table 17).

Complete observations from the start to the finish of a relocation are scarce and the following description is made by combining fragmentary records. From the start of attacks by *V. tropica*, the queen and workers of *Polistes* stop their building activity, though they continue to stay on the comb. After *V. tropica* have attacked the colony two or three times, some workers leave the nest and fly about to search for another nesting site nearby. When a suitable site is found not far from the original nest the scout workers settle

Table 17. The fate of *Polistes jadwigae* nests attacked by *Vespa tropica*, 1964-1975.

Period*	No. of nests attacked	Reconstruction at another site	Abandonment or disappearance	Aggregation around the nest site
I	4	2(50.0%)	2(50.0%)	0
II	192	171(89.1%) (159)(82.8%)**	21(10.9%)	0
III	75	8(10.7%)	1(1.3%)	66(88.0%)
Total	271	181	24	66

\* See Table 15.

\*\* Number of nests reattacked by *V. tropica* after reconstruction.

on the place and spend most of their time resting on it with occasional returns to the original nest. With the start of searching for a new nest site, the workers in the original nest stop building activities and the queen also stops oviposition. Then, they leave to search for the new nest site, which is usually situated in a sheltered place or in a bush. About a day after the arrival of the queen the workers usually start building a new nest and the queen begins to lay eggs.

The distance between the two nests was mostly within 1-3m, but reached 4m at the maximum. After they reconstruct a new nest, most of the workers frequently visit the original nest for several days, though they never reuse the abandoned nest even if *V. tropica* stop attacking it. However, 159 out of 171 nests (93.0%), which had been reconstructed during early June to mid-July, were reattacked by *V. tropica* before they produced new queens and males. On the other hand, after emergence of sexuals, 88.0% of total nests attacked by *V. tropica* did not construct a new nest, and all the adult wasps remained on or near the empty nest until disintegration in September.

### 3. Group predation by *Vespa mandarinia* on nests of honeybees and social wasps

It is well-known that *Vespa mandarinia* attacks bee hives in mass and causes serious damage to honeybee colonies in Japan (OKADA 1967, MATSUURA and SAKAGAMI 1973). The attack by *V. mandarinia* are not limited to the honeybee but are made also on nests of other lesser social wasps. The habits of this hornet are quite different from those by other *Vespa* species, as the former causes catastrophic damage to the victim's colony while the attack by congeneric species is restricted to individual hunting, with only minor effects. In this section some of the peculiarities of attacks by *V. mandarinia* are described.

#### 1) Visits by *Vespa* species to the apiaries

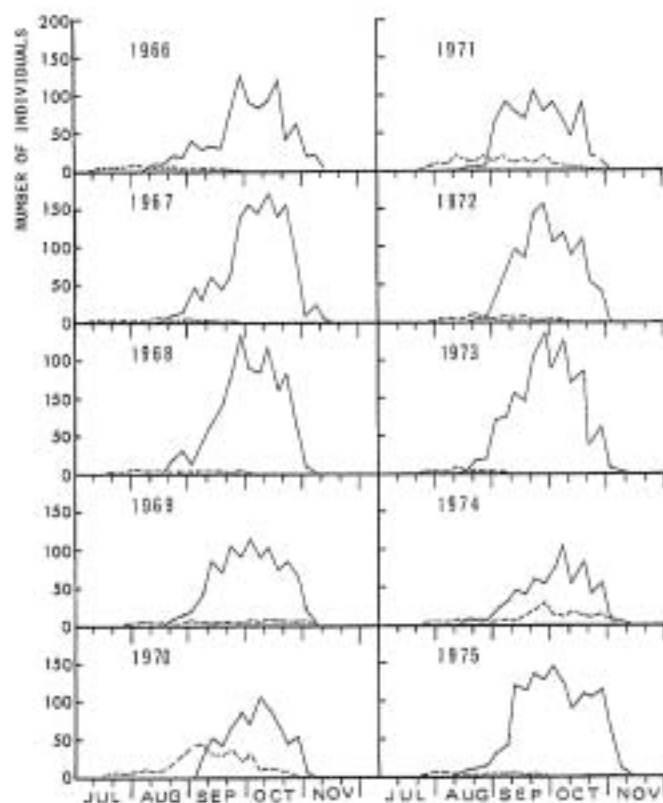
Various species of *Vespa* prey upon honeybees and lesser social wasps as their protein food (Table 13). Table 18 shows the frequency of visits to apiaries by five *Vespa* species, estimated from the number of specimens captured in hornet traps at an apiary in Kibi for a ten-year period. Among the species visiting the apiary, *V. mandarinia* and *V. simillima* were found to be important, and the former species was overwhelmingly more abundant than the latter one. However, there was a strong tendency for the ratio of visits by *V. simillima* to the apiary to increase in compensation when those by *V. mandarinia* decreased in some years. *V. simillima* rarely frequented the apiaries having been visited by *V. mandarinia*. Even when visiting, they were chased away or attacked by *V. mandarinia*, which attempted to catch *V. simillima*, and if successful, took it back to the nest.

The relative abundance of these two species may vary according to locality. In southern Japan both *V. mandarinia* and *V. simillima* seem rather abundant and the number of the latter species visiting apiaries rarely exceeds that of the former, but the situation is frequently reversed in northern Japan where *V. mandarinia* is regarded as less common than *V. simillima*, as reported MATSUURA and SAKAGAMI (1973).

Three other species, *V. analis*, *V. crabro* and *V. tropica*, were scarce: of these, *V. crabro* and *V. analis* actually hunted honeybees at the apiary, but they were of minor importance as pests. In the case of *V. tropica*

Table 18. Number of *Vespa* species captured in hornet traps attached to hives at an apiary in Kibi for a 10-year period.

Year	No. of <i>Vespa</i> species										Total no.
	<i>mandarinia</i>		<i>simillima</i>		<i>anis</i>		<i>crabro</i>		<i>tropica</i>		
	No.	%	No.	%	No.	%	No.	%	No.	%	
1966	970	93.6	49	4.7	10	1.0	1	0.1	6	0.6	1,036
1967	1,320	96.8	24	1.8	11	0.8	2	0.1	5	0.4	1,364
1968	1,324	96.4	19	1.4	21	1.5	2	0.1	8	0.6	1,374
1969	943	91.6	68	6.6	11	1.1	2	0.2	5	0.5	1,029
1970	700	65.8	340	32.0	16	1.5	1	0.1	7	0.7	1,064
1971	834	80.6	182	17.6	7	0.7	1	0.1	11	1.1	1,035
1972	1,115	93.9	58	4.9	9	0.8	1	0.1	4	0.3	1,187
1973	1,434	97.8	14	1.0	10	0.7	2	0.1	7	0.5	1,467
1974	706	70.0	288	28.6	8	0.8	3	0.3	3	0.3	1,008
1975	1,375	96.6	30	2.1	12	0.8	1	0.1	6	0.4	1,424
Total	9,294	88.2	1,050	10.0	115	1.1	16	0.2	62	0.6	10,537

Fig. 43. Phenology of *Vespa mandarinia* workers (—) and other *Vespa* species (-----) captured in the traps attached to 20 hives at an apiary in Kibi for a ten-year period. The hornets were counted every five days.

some workers occasionally visited the apiary and were captured in hornet traps, but so far no attack by this species has been confirmed though this species is regarded as a harmful hornet to honeybees in India (SUBBIAH and MAHADEVAN 1957).

## 2) Phenology of attack to apiaries

Visits by *Vespa* species to apiaries except for *V. mandarinia* continued from May to November, occasionally more abundant in mid-September but not forming a definite peak as in *V. mandarinia* (Fig. 43). In contrast to other *Vespa* species, visits by *V. mandarinia* were seasonally well delimited. No queens or workers visited apiaries until mid-August. The visits to apiaries became constant and gradually increased thereafter, reached a peak in late September to mid-October, with the number of daily visits being 30–50 individuals per apiary, which was estimated from the sum of the numbers of hornets daily killed and trapped. Numbers of *V. mandarinia* workers declined sharply after late October in most years, and no workers appeared in late November though they still continued their nesting activity. The rapid decrease of visits to the apiary is closely related to the emergence of sexuals in their nests after late October, because workers spend labour much more in collecting liquid food for the males and new queens than in hunting for the larvae.

## 3) Phenology of attack on other social vespine species

All the attacks on other social vespine species by *V. mandarinia* were observed from late August to early November (Table 19), and the peak of predatory activity occurred in late September to mid-October, which

Table 19. The time and number of nests of social wasps attacked by *Vespa mandarinia*, 1965–1975.

Species	Jul.			Aug.			Sep.			Oct.			Nov.			Total no. of nests attacked
	E	M	L	E	M	L	E	M	L	E	M	L	E	M	L	
<i>Polistes</i> spp.	0	0	0	0	4	1	1	0	0	0	0	0	0	0	0	6
<i>Vespa similima</i>	0	0	0	0	1	7	8	11	13	16	14	9	5	0	0	84
<i>Vespa analis</i>	0	0	0	0	2	2	3	8	9	8	4	3	1	0	0	40
<i>Vespa crabro</i>	0	0	0	0	0	0	0	2	2	1	1	0	1	0	0	7
<i>Vespa tropica</i>	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1*
<i>Vespula flaviceps</i>	0	0	0	0	0	6	5	10	12	18	11	7	8	0	0	77
Total no. of nests attacked	0	0	0	0	7	16	17	32	36	43	30	19	15	0	0	215

\* Nest kept at the apiary. E, M and L mean early, mid- and late in each month, respectively.

coincides with that of honeybees as mentioned above. On the other hand, the numbers of workers and combs in vespine wasps reach maxima in September to October, and the lower combs contain larvae and pupae of sexuals, which offer a large quantity of protein food for *V. mandarinia*. Probably this may partly explain the concentrated predation by *V. mandarinia* on honeybees and other social vespine colonies in these months.

However, why *V. mandarinia* does not visit apiaries or other vespine nests until mid-August is still unsolved. It may have some preferred prey which decrease in late summer, or some quantitative change of protein requirement may appear in parallel with the start of rearing sexuals. Alternatively, the attack on apiaries and vespine nests may be started only after a sufficient number of workers have emerged. At present there is little concrete evidence to test these assumptions.

## 4) Predatory habits

The attack by *V. mandarinia* is divided into three successive phases, hunting, slaughter and occupation both on honeybees and other vespine nests.

## a) Hunting phase

In the case of beehives the behaviour of *V. mandarinia* in the hunting phase is basically the same as that of *V. similima* and other species, which attack the prey only by individual hunting, giving no acute and catastrophic result. Main differences are:

(1) *V. mandarinia* workers are less skillful in catching bees in flight. They await their chance, sitting near hive entrances or on hives more persistently than other species.

(2) They are more apt to seize bees with the mandibles. Once counter-attacked and gnawed by a bee, the hornet flies away from the hive, removes the bee with its legs in the air and immediately bites it to death.

In the hunting phase, therefore, each worker of *V. mandarinia* repeats a chain performance of visiting—waiting—catching one bee and preparing a meat ball from the prey's mesosoma—carrying the ball back to the nest. At a hive which counter-attack weakly, 2–5 hornets may visit synchronously or alternately. They invariably repeat the same performance, never, leaving the corpses of the bees in the apiary as in the next phase. So long as the attack remains in the hunting phase, the damage to hives does not exceed that by *V. simillima* very much, or is often less because of the lower frequency of visits reflecting its smaller nest population, and less agile behaviour than *V. simillima*.

Attacks on nests of other hornet species also start with the hunting phase. The worker of *V. mandarinia* hovers around the other vespine nest for quite a long time and she suddenly pounces upon an individual victim at or near the nest entrance. After falling down on the ground in combat, the victim is usually killed with the mandibles and the mesosoma is transformed to a meat ball and carried back to the nest, as with a honeybee. However, the attacked species, especially *V. analis* and *V. crabro*, occasionally kills the *V. mandarinia* by counter-attacking with its sting. In large nests of *V. simillima* and *V. crabro* many workers usually take to the air at the arrival of *V. mandarinia* and chase away the invader so that even the hunting phase is only intermittent and seldom shifts to the slaughter phase. In nests of these species that are small due to delayed development or orphanage, and nests of *V. analis* which never reach a large size, the hunting phase can shift to slaughter.

The hunting phase can continue for an indefinite time with or without shifting to the next phase. The shift to the slaughter phase partly depends on the distance between the apiary or the vespine nests and the *V. mandarinia* nest. When the victim's nest is located near the *V. mandarinia* nest and receives constant visits by workers of the same nest, the shift is nearly certain, while at an apiary or nest remote from the outskirts of mountains and hills, where most *V. mandarinia* nests are concentrated the frequency of visits is low and the shift to the next phase is rather rare.

#### b) Slaughter phase

Once the attack shifts to the second phase, the behaviour of *V. mandarinia* workers changes drastically. In the case of beehives, they do not visit different hives alternately as in the hunting phase, they concentrate attacks on a particular hive (Fig. 44), ignoring others even if placed side by side. If one captures

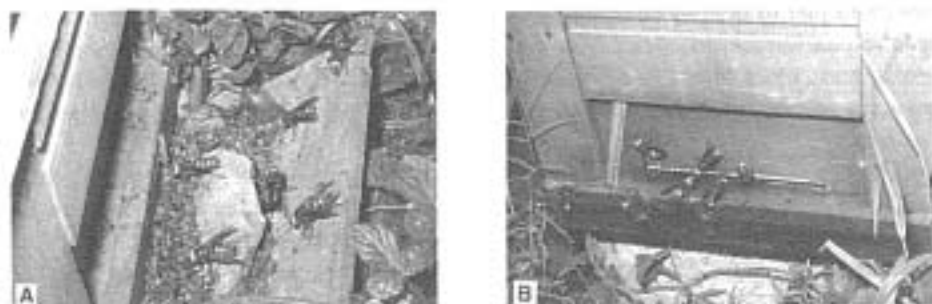


Fig. 44. Attacks by *Vespa mandarinia* on a hive of *Apis mellifera*: A, slaughter phase; B, occupation phase.

a hornet at this phase and liberates it near the apiary, she immediately returns to the victim hive to recommence the attack. Once the victim hive is chosen, another hive is never substituted throughout this and the next phase.

The attack in this phase is a simple repetition of slaughter. Usually staying near the hive entrance, each hornet bites to death each bee approaching her for counter-attack (Fig. 45). The corpses are left on the ground nearby without being carried back to the nest. Once a bee bites her body, the hornet often soars up, removes the bee in the air with its legs, bites her to death, throws down her corpse and returns to





Fig. 45. *Vespa mandarinia* worker biting a honeybee.

the hive entrance to recommence the slaughter. The use of the sting to kill bees has so far never been observed. The number of hornets attacking at this phase is always more than two, and up to 50, although they do not work cooperatively. The slaughter can be started from early morning to evening, but usually starts in the forenoon. Once slaughter develops, participating hornets do not return to the nest until the end of the phase. Or, when the phase continues to the next, hornets return to their nest at sunset but reattack the victim hive on the next day in the early morning.

Individual marking shows that hornets participating in slaughter at a hive always belong to the same nest. Occasionally alien hornets appear at the apiary in the midst of slaughter, but they are chased away by 'legitimate' owners with or without combat. On the other hand, newly arrived hornets of the same nest participate directly in slaughter, omitting the hunting phase.

The duration of slaughter is variable according to the number of hornet participants and the intensity of the defense. The defense always appears during the initial part of the phase and is mostly initiated by bees of guard or foraging ages while foragers returning to the hive often do not participate in its defense but leave the hive. When more than ten hornets make the slaughter, counter-attacks suddenly cease one to six hours after the start of the phase when the population of the victim hive has been decreased considerably. Many beekeepers have bitter experiences of losing their hives during their absence from apiaries of only one hour or even 30 minutes. Many surviving bees leave the hive but some remain without resistance. Because hornets in the slaughter phase do not return to the nest nor chew the killed bees, food deficiency occurs as slaughter continues, resulting in the appearance of frequent and persistent food exchange at the apiary. In extreme cases, the hornets starve to death during a prolonged slaughter.

The number of bees killed by hornets varies according to the size of victim colonies, number of hornets, and intensity of counter-attacks. In southern Japan, the hives managed by the non-migratory apiculture system involves 15,000–30,000 bees in August to October. Visits by 20–30 hornets usually result in deaths of 5,000 to 25,000 bees during one to six hours, unless the attack is artificially interrupted. Hornet deaths during the slaughter phase are usually only one or two. In one instance, about 25,000 out of 30,000





Fig. 46. Attacks by *Vespa mandarinia* on *Vespa similima* nest: A, *V. mandarinia* workers pulling out a pupa in the occupied nest of *V. similima*; B, shambles after a battle.

inhabitants were killed during three hours by 30 hornets while only two hornets were killed by bees. This means that each hornet killed approximately one bee every 14 seconds.

In the case of other *Vespa* nest combat in this phase was naturally much more severe than in attacks on *Apis mellifera* (Fig. 46,B). Several workers of the victim species (or sometimes only one in *V. analis*) confront each *V. mandarinia* in flight or on the nest entrance. The two opponents fall to the ground and fight violently with each other, using mandibles, legs and stings. The slaughter phase lasts several hours or continues to the next day. In all so far observed cases, the slaughter phase always proceeds to the occupation phase.

In *Vespula*, about ten hornets can completely conquer the victim nest during one hour and occupy it with the loss of only one to two individuals. Adult victims are mostly killed with the mandibles, not by stinging. The counter-attack by *Vl. flaviceps* seems not so severe as that made by *Apis mellifera*. Usually few dead of both predator and prey are found at the nest entrance. In a nest occupied by about 20 *V. mandarinia* worker, several tens of *Vl. flaviceps* were still alive in the nest, and departures and returns of a few *Vl. flaviceps* workers were observed. It is an open question whether the slaughter phase is here so distinct as in the case of the honeybee.

The causal mechanism underlying the shift from hunting to slaughter phase is as yet unknown. As the shift usually appears after hornets have received intense counter-attacks, the latter may release the change of their behaviour. However, the shift develops only when more than one hornet of the same nest participates in hunting. Therefore, it is plausible that some interindividual relation stimulates the slaughter. Moreover, the number of hornets often increases in the course of slaughter. Some beekeepers assume that the information brought by homing hornets during the hunting phase favours the arrival of other nest mates. However, there is still no positive evidence to confirm such an assumption. As the recognition of nest mates exists in *V. mandarinia*, it is conceivable that some stimulant is emitted by the individual shifting to slaughter phase, which evokes a concentration of further individuals to the place. The fact that hornets are attracted to the individuals killed and left at particular points seems to favour this assumption, but the problem is still open to critical studies.

#### c) Occupation phase

After the cessation of defense by the occupants and escape of survivors, hornets successively enter the victim hive or nest and occupy it. They pay little attention to some bees still surviving in the colony. Once the slaughter phase is attained, it invariably proceeds to the occupation phase unless artificially inhibited. Within the hive or nest each hornet walks over the combs, and opens a cocoon and pulls out the pupa (Fig. 46,A). Keeping it between mandibles, she flies away to a branch near the apiary or nest, removes unnecessary body parts and carries back the mesosoma of the pupa to her own nest. At first they prefer later stage pupae, then gradually shift to younger ones and finally to larvae, which are usually directly carried back without chewing. Soon after the slaughter phase, the corpses of victims and their own species are also prepared as meat balls and transported to the nest. But it ceases on the next day, probably because of putrefaction.

In this way, the occupied hive or nest is continuously visited by ten to several tens of hornets in the daytime for several days up to two weeks. Often some individuals pass the night in the victim's nest, not returning to their own nest.

*V. mandarinia* workers in the occupation phase change their disposition. The occupied hive or nest is guarded by some individuals sitting at the entrance (Fig. 44,B). The approach of men, dogs, other hornets of different species, and of the same species belonging to alien nests or any other large animals releases attacks by these guards. As in most social insects away from nests, *V. mandarinia* do not make such attacks on men during the hunting and slaughter phases, so that they can be beaten to death with wooden sticks, etc. at apiaries. In the occupation phase, however, this operation becomes difficult because of attacks by guards. Before attacking, each hornet often flies around the men or any animals approaching the occupied hive or nest and threatens them by a peculiar loud clicking produced by rapid opening and closing of the mandibles. This clicking is produced in all Japanese *Vespa* species at or near their nests,

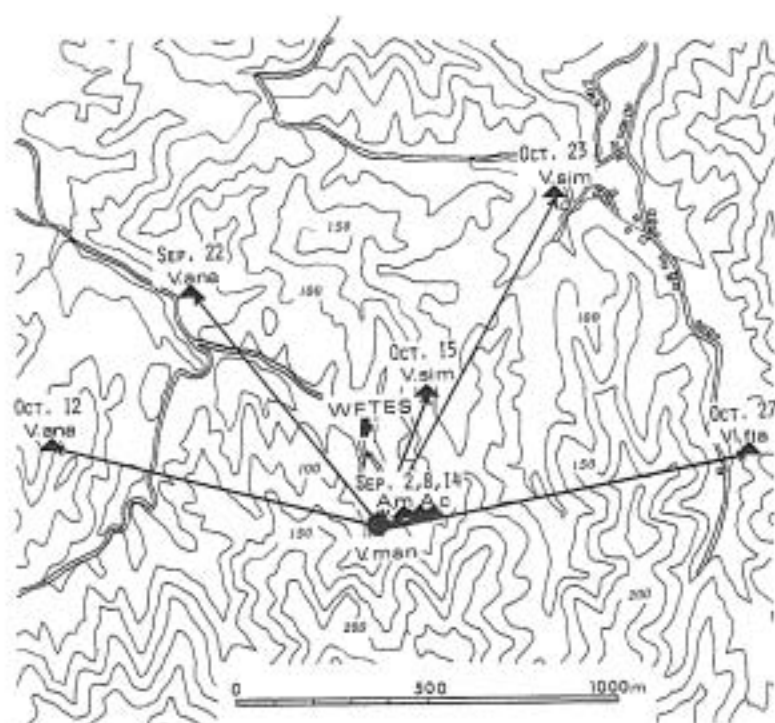


Fig. 47. Distribution of vespine nests and honeybee hives (▲) attacked by *Vespa mandarinia* (●) near and at the Wakayama Fruit Tree Experimental St.(WFTES) orchard and forests in 1972 with the date of the discovery of mass attack.

*V. sim*: *Vespa similima*; *V. ana*: *V. analis*; *Vl. fla*: *Vespa flaviceps*; *Am*: *Apis mellifera*; *Ac*: *A. cerana*.

Table 20. Number of vespine nests attacked by *Vespa mandarinia*, 1965-1975.

Species	No. nests observed (A)	Year												% of nests attacked
	No. nests attacked (B)*	'65	'66	'67	'68	'69	'70	'71	'72	'73	'74	'75	Total	
<i>V. similima</i>	A	2	10	5	9	6	24	17	21	9	7	8	118	13.6
	B	1	0	0	2	0	3	3	3	2	1	1	16	
<i>V. analis</i>	A	5	2	15	13	2	0	7	10	8	3	13	78	15.4
	B	3	0	0	0	0	0	1	5	1	1	1	12	
<i>V. crabro</i>	A	1	4	5	4	0	4	3	3	4	5	7	40	4.8
	B	0	1	0	0	0	0	1	0	0	0	0	2	
<i>VI. flaviceps</i>	A	7	6	5	7	6	5	5	6	8	8	5	68	50.0
	B	5	2	3	3	3	2	2	3	5	4	2	34	
Total	A	15	22	30	33	14	33	32	40	29	23	33	304	20.4
	B	9	3	3	5	3	5	7	9	8	6	4	62	

\* Number of nests observed only during the attacking period from mid-August to early November.

and is regarded as a habit characteristic of or prevalent in the genus. In *V. mandarinia*, it is produced not only at nests but also at the hives or nests occupied and frequently visited tree sap sources. This indicates its well developed territorial defense. The relative aggressiveness of various species to men at or near their own nests is ordered: *mandarinia* > *simillima* > *crabro* > *anis* > *tropica*.

Although occasional entries into hives are recorded for some other hornet species (*V. affinis* in Formosa by SONAN 1927; *V. sp.* in Afghanistan by SCHNEIDER and DJALAL 1970), a lasting occupation of victim hives is previously recorded only in *V. orientalis*. From the description by ISHAY et al. (1967), the presence of a distinct slaughter phase in this species is not clear. It would be interesting to observe how *V. orientalis* develops its occupation phase. Some beekeepers assume that the aim of hive occupation by *V. mandarinia* is to pillage the stored honey. But as far as my observations have determined, hornets destroy honey combs but rarely take honey to carry back to the nest. As seen from the observations on vespine nests, the main aim of occupation must be predation on pupae and larvae. Most observations cited in MATSUURA and SAKAGAMI (1973) on other *Vespa* species confirm the preference for the muscular mesosoma of the prey. This is in marked contrast to visits by *Vespula flaviceps* to apiaries; this species seeks mainly the stored honey. FREE (1970) showed that meso- and metasoma of honeybees are equally preferred by the European yellowjackets, *Vespula germanica* and *V. vulgaris*. This might indicate that *Vespula* is less predacious than *Vespa*. As shown in Table 12, *V. mandarinia* workers are especially fond of tree sap but do not frequent flowers except for some rare visits to *Cissus japonica* and *Ampelopsis heterophylla*. When diluted honey and tree sap are simultaneously offered, *V. mandarinia* invariably prefers the latter. These facts suggest that the stored honey does not form a principal objective of the hive occupation in the case of attack on *Apis mellifera*.

#### 5) Foraging distance

The flight radius of *V. mandarinia* is on the average 1–2 km, reaching a maximum of 8 km. The distance between a nest of *V. mandarinia* and apiaries or victim's nests is mostly 1–2 km (max. 2.5 km) and serious damage appears mainly at apiaries located less than 1 km from hornet nests (KOJIMA 1950, MATSUURA and SAKAGAMI 1973). Other vespine nests attacked are also mainly located less than 1 km from a nest of *V. mandarinia*. Fig. 47 shows the distribution of vespine nests destroyed near and at the Wakayama Fruit Tree Experimental Station's orchards and forests at Kibi in 1972. Of 8 nests of various *Vespa* and *Vespula* species within 1 km from a nest of *V. mandarinia*, a total of 5 nests were attacked and destroyed by workers of the same nest of *V. mandarinia*. As far as I knew, the workers of this nest exterminated two nests of *V. simillima*, two of *V. analis* and one of *Vespula flaviceps* during September and October. Furthermore, they attacked two hives of *Apis mellifera* and one hive of *A. cerana* which were located about 100 m away from their nest. These data show that *V. mandarinia* plays an important role in controlling other vespine nests in the neighbourhood of *V. mandarinia* nests.

#### 6) Ratio of vespine nests attacked and destroyed by *V. mandarinia*

Attacks on *Vespula* and *Vespa* nests have so far been observed only by *V. mandarinia*. Table 20 shows the number of nests which were attacked and destroyed by the hornet during an 11-year period from 1965 to 1975. The ratio of nests destroyed by *V. mandarinia* reached 50.0% (34/68) of total nests of *Vespula flaviceps* observed during the period from mid-August to early November in and near Kibi. On the other hand, in cases of *Vespa* species, the nests destroyed by *V. mandarinia* were only 4.8% (2/40) in *V. crabro*, 13.6% (16/118) in *V. simillima* and 15.4% (12/78) in *V. analis*, of the total nests observed during the attacking period of *V. mandarinia*. Large nests of *Vespa* can resist the attack and inhibit it at the incipient stage of the hunting phase, rarely the slaughter phase. Judging from the data shown in Tables 19 and 20, together with other observations in the field, the relative resistive ability of vespine wasps against *V. mandarinia* is ordered: *crabro* > *simillima* > *anis* > *V. flaviceps*, though it may vary according to sizes of victim colonies, number of foraging hornets and intensity of counter-attacks.

Attacks on nests of *V. tropica* have so far not been confirmed under natural condition. This may be due to the relative rarity and short annual cycle of this species, which reaches the dissolution phase before the attacks by *V. mandarinia* intensify. Once its nests are discovered and attacked, it is certain that this mildest hornet making the smallest nests would be easily conquered by *V. mandarinia*. Two small nests reared

in my vespiary were attacked and occupied each by only three workers of *V. mandarinia* on 19th September, 1973. No intraspecific attack of *V. mandarinia* has so far been confirmed either directly or indirectly by the sudden appearance of numerous dead near the nests.

7) Attack on hives of the Japanese honeybee, *Apis cerana*

The foregoing description shows that nests of other social wasps are victimized by *V. mandarinia*. Only large nests of *V. simillima* and *V. crabro* can resist the attack and inhibit it at the incipient stage of the hunting phase. Meanwhile, there is another social insect, the bee *Apis cerana japonica* Fabricius, the eastern-most and largest subspecies of the Asiatic honeybee which may be attacked.

Since TOKUDA (1924) it is well known that this species avoids the damage by retreating within its nests at the arrival of *V. mandarinia*. Closer observations confirmed that *A. cerana* defended itself well against the giant hornet not only by a passive retreat but also by a particular method. The following observations were made with colonies kept in a hive adopted in and near Kibi, a wooden box with several small entrance holes below, which was designed by Mitsuichi SADA, the father of Japanese Apiculture, who lived in Arida near Kibi.

At the arrival of a hornet, departures from the hive abruptly cease. The shimmering, a warning sound characteristic of the species (SAKAGAMI 1960), is repeatedly emitted from the hive. Homing foragers keep a distance from the hornet and quickly enter into the hive through holes remote from the enemy (Fig. 48). By this rapid retreat with no solitary counter-attack, the hornet usually relinquishes her attempt and leaves.



Fig. 48. Beginning of the formation of a circle of *Apis cerana* around a *Vespa mandarinia* worker attempting to invade the hive.

If the hornet persists, however, numerous bees appear from the entrances remote from it. Never flying nor darting solitarily to the hornet as *A. mellifera* does, some bees approach the hornet, directing their heads to the enemy, raising their metasomal tips and vibrating the wings. Thus, a circle of bees is formed around the hornet. The attempt to seize bees by the hornet seldom succeeds for the movements of bees are incomparably more agile than their European cousins. Meanwhile, one bee pounces rapidly upon the head of the hornet. Nearly synchronously all others in the circle rush upon the enemy and other bees near the entrance concentrate on the place. About 10–15 seconds after the attack by the first bee, the hornet is covered thickly by several tens to several hundreds of bees. Shimmering in the hive, repeated since the arrival of the hornet, ceases and departure of foragers recommences. The bees covering the hornet keep their positions



for more than 20 min. with little motion. The same mass defense is also applied to the occasional hornet that enters a hive. The corpse of the hornet shows no external injury; she is seemingly killed by stings.

Thus, the attack by *V. mandarinia* is interrupted at the initial part of the hunting phase. The hornet either is killed or abandons the attack which does not develop into its subsequent phases. I have had the opportunity to observe only a few instances of the mass defense described above. But the lack of sufficient observations is simply due to the rarity of catastrophic damage by *V. mandarinia*. According to the experience of me and several beekeepers, *V. mandarinia* never visits the hives of *A. cerana* placed near those of *A. mellifera*. Among about 300 hives and more than ten natural nests of *A. cerana* observed by me in the areas where *A. mellifera* is also kept, no instance of slaughter or extermination by *V. mandarinia* has been recorded. Several beekeepers possessing *A. cerana* hives, including one who has kept several tens of colonies at the same time, invariably recorded the absence of catastrophic damage by *V. mandarinia*.

The efficiency of both attack and defense between predator and prey must be envisaged in its equilibrium, changing by situations. If a colony of *A. cerana* is kept in a hive with a wide entrance space as used for *A. mellifera*, which makes invasion of several hornets possible, the effective defense described above may be difficult. One instance of attack by *V. mandarinia* on a colony of *A. cerana* resulting in mild damage was noted on 22nd October 1972. Three workers of *V. mandarinia* were flying around in front of a *A. cerana* colony, which was kept in a hive with an ample entrance space. After killing these hornets, the hive was inspected and the following dead were discovered: 4 hornets in front of hive, 4 within the hive and about 80 bees in front of the hive. The hornets' nest was located about 100m away. During September and October, the workers of this same nest exterminated two nests of *V. similima*, two of *V. analis* and one of *Vespa flaviceps* (See Fig. 47).

Nevertheless, it is certain that *A. cerana* has developed two fairly effective defensive techniques, neither possessed by *A. mellifera*, one being passive—the absence of solitary counter-attacks, and the other, active—a rapid mass attack and a long contact with *V. mandarinia*. This skillful defense contrasts sharply with its inability to resist pillage by *A. mellifera*: when colonies of both species are kept in the same place, in most cases *A. mellifera* ultimately pillages and exterminates the colony of *A. cerana* (SAKAGAMI 1959). Thus, the introduction of *A. mellifera* to Japan evoked a curious triangular relation among the three species during a century.

Serious damage to bee hives by hornets, including *V. mandarinia magnifica*, are recorded in India (*Apis cerana indica*: SMITH 1960), Indochina (*A. c. javana*: TOUMANOFF 1939) and Afghanistan (*A. c. ssp.*: SCHNEIDER and DJALAL 1939). KLOFF and SCHNEIDER (1970) described a defensive behaviour of *A. cerana* ssp. in eastern Afghanistan to *Vespa* sp.: At the arrival of a hornet, 30 bee workers form a dense mass at the nest entrance, each changing its orientation to the hornet according to the movement of the latter. On the approach of the hornet beyond a critical distance, bees raise their metasomas and lower their heads, together with the production of shimmering. The hornet only catches bees leaving the defensive mass. In general the observation cited corresponds to my observation but the initial retreat and mass counter-attack I observed are not mentioned. Considering this absence of its description, together with the serious damage to *A. cerana* by *Vespa* in the same area, the defensive behaviour in the Afghan population seems less perfect than in Japan. It is important to make further comparative observations on the defensive behaviour of *A. cerana* in various areas.

ISHAY et al. (1967) refer to the mass defense made by the local bee race in Israel: "The local bees protect themselves against hornets by forming dense clumps at the entrance of the hive. In such instance, a hornet, in order to capture a bee, must first detach it from the rest, a rather difficult feat which is rarely successful. There is another danger that the overly venturesome hornet, in coming too close to the apian phalanx, may occasionally become the victim of its prey and be stung to death by the massed bees." It is noteworthy that a mass defense, quite comparable to that of *A. cerana cerana*, is thus confirmed in a race of *A. mellifera*. The similarity may be explained either by the parallel acquisition of a similar defensive mechanism or by the loss of such in some members of the subgenus *Apis*, as I have thus far no information on *A. dorsata*, *A. florea* and their relatives, i.e., the subgenera *Megapis* and *Micrapis*. The shimmering seems to offer another



instance of the presence of a discrete behavioural character in races of both species, for BUTLER (1954) recorded a trace of this habit in *A. mellifera cyprica* in Cyprus. Further comparative observations on behaviour both of hornets and honeybees may throw light on reciprocal evolution of attack and defense mechanisms in these insects.

Judging from these observations several possibilities exist to explain the discrepancy between these records and observations in Japan: 1) Lower defensive ability in southern populations of *A. cerana* against *Vespa*. 2) Presence of some efficient hunting behaviour in the *Vespa* species cited. 3) Presence of some particular situations that facilitate the attack, occurring either ecologically (seasonal correspondence of colony cycles of prey and predator, etc.) or artificially (condition created by apicultural procedures, etc.). Further comparative observations in these areas are required. It might be worth studying the use of appropriate hives, especially those with the entrance not too wide.

#### 4. Intra- and inter-specific relationships at food sources

Various species of hornets obtain carbohydrates from tree sap. At the tree apertures where the secretion is abundant, they assert their territorial right by driving away visitors of the same or different species from the place. If two or more individuals of the congeneric or different species are found at or around the same place, certain rules are recognized among them.

This section describes the dominance behaviour in hornet which is analogous to the "peck order" found in the domestic fowl (SCHJELDERUP-EBBE 1922).

##### 1) Dominance relationships among queens visiting tree sap

The post-hibernating queens search for tree sap before devoting themselves to the nesting sites. Table 21 shows the frequency of visit and the feeding times of 18 marked individuals of four *Vespa* species that visited a tree aperture during three days at the beginning of May in 1967, and in Fig. 49 is given one example concerning the activities of tree sap intake observed among 12 queens and 2 stylopized workers of *V. mandarinia*, 2 queens of *V. crabro* and each one queen of *V. analis* and *V. similima* on May 5th,

Table 21. Length of time(in min.) spent taking tree sap by each individual visiting the tree aperture during three days at the beginning of May 1st in 1967.

Species and individual marked*	Frequency of visits	Frequency of feeding	Total time for feeding	Average each feeding time	Time for nonfeeding
ma 12	5	5	103	21.0	0
ma 1	11	9	158	17.5	0
ma 5	13	9	79	8.8	1
ma 4	9	8	82	10.0	1
ma 9	11	8	31	4.0	128
ma 2	10	6	42	7.0	46
ma 3	18	5	28	5.6	126
ma 6	9	10	59	3.9	286
ma 11	6	2	4	2.0	239
ma 7	1	1	1	1.0	153
ma 8	2	0	0	0	6
ma 10	7	0	0	0	29
ma 1	4	0	0	0	129
ma 2	3	0	0	0	153
cr 1	8	0	0	0	198
cr 2	2	0	0	0	132
an 1	3	0	0	0	233
xa 1	2	0	0	0	0

\* ma 1-12: queen of *V. mandarinia*, ma 1-2: stylopized worker of *V. mandarinia*, cr 1-2: queen of *V. crabro*, an: queen of *V. analis*, xa: queen of *V. similima*.

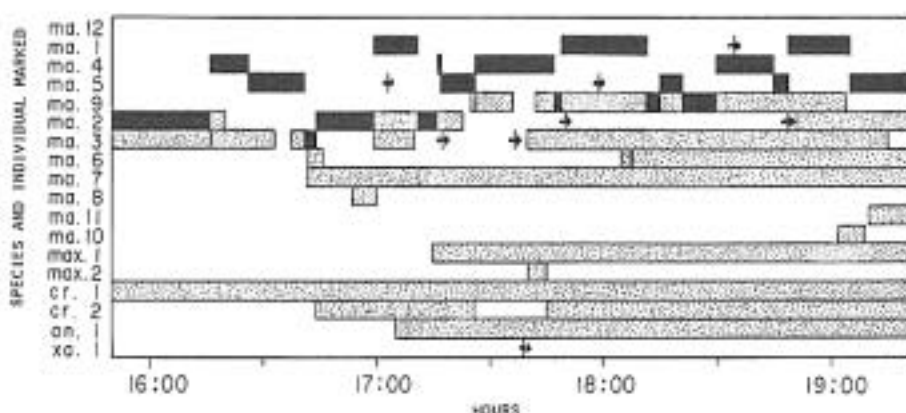


Fig. 49. Activities of tree sap intake observed among 18 marked individuals of 4 species *Vespa* that visited a tree aperture in the daytime of May 5th, 1967.

Black rectangles indicate the occupation of the tree aperture. Spotted rectangles indicate staying around the tree aperture without feeding. Arrows indicate flying away soon after flying around the tree aperture.

1967 at the same place. There is a significant difference in the feeding time of each individual and it is certain that each queen occupies the tree aperture according to the relation of the order among them. In the daytime the tree aperture exuding sap was always occupied by a single queen, surrounded by others that were unable to take the tree sap. They were driven back without any counter-attack, by the threatening of the occupant with mandibles widely opened, whenever they tried to approach the aperture.

Feeding individuals changed places when the first became fully engorged and flew away, or when she was driven off from the tree aperture by a superior individual arriving from another place (Fig. 49). When the same or another species visited a tree aperture already occupied by a feeding individual, the response of the visitor to the occupant was one of the following: A. Alighting on the position at a distance of 5-6cm from the occupant, after flying around the tree aperture, B. Flying away soon after flying around the tree aperture, C. A severe combat with mandibles and stings between both individuals soon after alighting on near the tree aperture; the victor begins to take tree sap and the defeated, on the contrary, flies away, D. An immediate change over from the occupant to the visitor without any combat; the occupant gives up the position and retreats or flies off.

Judging from the relation of the order of individuals referred to later, the dominance relations between visitor and occupant in the above cases are as follows: Both in A and B the visitor is inferior to the occupant, and their order is relatively close to each other in B while not very close in A; only two examples of C were observed in 1967, and it is conceivable that they are of the same rank; on the contrary, in D the visitor always has a higher rank than the occupant.

The inferior and superior types of behaviour were observed not only among occupants and non-occupants but among non-occupants surrounding the tree aperture. The inferior individuals retreated when perceiving the approach of a superior one which frequently threatened with opened mandibles, and so each individual took up a position away from the others, forming an approximately uniform spatial distribution around the aperture. In Table 22 are indicated the frequencies of dominance and subordination among marked individuals, both intra- and interspecifically, in mutual attacks and Table 23 shows the frequency of retreating behaviour among them.

On the basis of these observations given in Fig. 49, and Tables 21, 22, 23, it is certain that there is a distinct linear dominance relationship among the queens of *Vespa* species visiting tree sap. The following

Table 22. Frequencies of dominance and subordinating relations among marked individuals of five *Vespa* species (cf. Table 21) visiting tree sap in the daytime during May 3rd-8th, 1967.

Individual marked	ma 12	ma 1	ma 5	ma 4	ma 9	ma 2	ma 3	ma 6	ma 11	ma 7	ma 8	ma 10	max 1	max 2	cr 1	cr 2	an 1	Total frequency of subordinating
ma 12	—	0	0	0	0	0	0	0	0	*	0	0	0	*	0	0	*	0
ma 1	2	—	2	4	0	0	0	0	0	0	0	0	0	0	0	0	0	8
ma 5	2	2	—	0	0	0	0	0	0	0	*	0	0	0	0	0	0	4
ma 4	5	0	1	—	0	0	0	0	0	0	*	0	0	0	0	0	0	6
ma 9	4	18	5	9	—	0	1	0	0	0	0	0	0	0	0	0	0	37
ma 2	2	4	3	2	0	—	0	0	0	0	0	0	0	0	0	0	0	11
ma 3	6	7	12	5	2	11	—	0	0	0	0	0	0	0	0	0	0	43
ma 6	17	22	8	6	4	10	7	—	1	0	0	0	0	0	0	0	0	75
ma 11	7	13	0	8	7	1	1	18	—	0	0	0	0	*	0	0	0	55
ma 7	*	1	1	0	0	1	1	3	0	—	0	0	1	0	0	0	0	8
ma 8	5	0	*	*	0	4	0	1	0	0	—	*	*	*	0	0	0	10
ma 10	1	0	0	1	0	0	0	2	0	0	*	—	0	1	0	0	0	5
max 1	1	0	0	0	1	1	0	2	0	0	*	1	—	0	0	0	0	6
max 2	*	0	0	0	0	0	0	3	*	0	*	0	0	—	0	0	0	3
cr 1	1	4	8	4	0	8	4	0	0	2	0	0	1	0	—	1	3	36
cr 2	0	1	1	0	0	1	1	0	0	0	0	0	1	0	0	—	0	5
an 1	*	0	0	0	0	0	1	2	0	1	0	0	1	3	1	0	—	9
Total frequency of dominance	55	72	41	39	14	37	16	31	1	3	0	1	4	4	1	1	3	

\* No chance of encounter.

Table 23. Frequencies of retreating behaviour among queens and styloped workers of *Vespa* species (cf. Table 21) visiting tree sap during May 3rd-8th, 1967.

Individual marked	ma 12	ma 1	ma 5	ma 4	ma 9	ma 2	ma 3	ma 6	ma 11	ma 7	ma 8	ma 10	max 1	max 2	cr 1	cr 2	an 1	Total frequency of dominance
ma 12	—	0	0	2	2	0	0	2	2	*	0	0	0	*	0	0	*	8
ma 1	0	—	1	0	0	0	2	5	0	0	0	0	0	0	0	0	0	8
ma 5	0	0	—	2	1	1	2	0	0	0	*	0	0	0	0	0	0	6
ma 4	0	0	0	—	3	1	0	2	0	0	*	0	0	0	0	0	0	6
ma 9	0	0	0	0	—	1	1	3	1	0	0	0	0	0	0	1	1	8
ma 2	0	0	0	0	0	—	1	1	1	0	0	0	0	0	0	0	0	3
ma 3	0	0	1	0	0	0	—	4	2	0	0	0	0	0	3	0	1	11
ma 6	0	0	0	0	0	0	0	—	12	2	0	1	1	3	4	0	2	25
ma 11	0	0	0	0	0	0	0	1	—	0	0	1	0	*	0	0	1	3
ma 7	*	0	0	0	0	0	0	0	0	—	0	0	0	0	3	0	2	5
ma 8	0	0	*	*	0	0	0	2	0	0	—	*	*	*	0	0	0	2
ma 10	0	0	0	0	0	0	0	0	0	0	*	—	1	0	0	0	0	1
max 1	0	0	0	0	0	0	0	0	1	1	*	0	—	1	0	0	2	5
max 2	*	0	0	0	0	0	0	0	*	0	*	0	0	—	5	0	0	5
cr 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	4	4
cr 2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	—	0	0
an 1	*	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	—	1
Total frequency of retreat	0	0	2	4	6	3	6	30	19	3	0	2	2	4	16	1	13	

\* No chance of encounter.

order could be observed as an intraspecific dominance relationship among the queens and the styloized workers of *V. mandarinia* who visited the tree aperture at the beginning of May in 1967:

$$\text{ma12} - \left\{ \begin{array}{c} \text{ma4} - \text{ma1} \\ \text{ma5} \end{array} \right\} - \text{ma9} - \text{ma2} - \text{ma3} - \text{ma6} \left\{ \begin{array}{c} \text{ma8} \\ \text{ma7} \\ \text{ma11} - \text{ma10} \end{array} \right\} - \text{ma1} - \text{ma} \times 2$$

Interspecific dominance relationship among queens visiting tree sap is, though greatly influenced by the individual disposition, generally as follows: *mandarinia* - *crabro* - *analis* - *simillima* - *tropica*.

Each individual takes tree sap according to the order mentioned above. The queen hornet ma 12 of *V. mandarinia* with the top rank could occupy the tree aperture and take her fill of tree sap at any time when she visited on both May 6th and 8th. The next position was occupied by three individuals, ma 1, ma 4 and ma 5, all *V. mandarinia* among which an interesting triangular order was noticed. Each of these three queens could take tree sap in the absence of superior ones, but would fly off when a superior one arrived.

Individuals under the above four queens in their order usually spent much time near the tree aperture waiting for an opportunity when the occupant would take her fill of tree sap and fly off. The relation of order among four queens at the bottom, ma 11, ma 10, ma 7 and ma 8, was not clear, because these individuals had little opportunity of taking tree sap in spite for waiting patiently during the daytime (Table 21 and Fig. 49). However, even individuals at the bottom could take their fill of tree sap in the evening as mentioned below.

## 2) Behaviours of overwintered queens in the evening

The hibernated queens take tree sap not only during the daytime but also in the evening for several days soon after emerging from their hibernacula. In 1966 *Quercus* trees began to secrete tree sap on April 25th and hibernated queens of *Vespa* species visited the tree aperture where the secretion was abundant. Their activity of tree sap intake in the evening continued until May 3rd. Thereafter not a single queen could be observed at the tree aperture in the evening in spite of abundant secretion. One evening the tree aperture was occupied by a queen, and within about 10cm from the aperture several queens of the same or different species waited for an opportunity to take the sap until the occupant left. In the evening an occupant is dominant over the others and is able to take tree sap fully without disturbance by superior individuals, since no other queens of *Vespa* species arrive from other places in the evening. When the others approached the tree aperture she threatened with her mandibles and drove them away as observed in the daytime. The dominance relationship among the occupant and non-occupants and among non-occupants was also observed during the evening. Table 24 indicates the frequency of dominance behaviour among

Table 24. Frequencies of dominance and subordinating relations among queens of *Vespa mandarinia* and *V. crabro* visiting tree sap in the evening on May 1st, 1966.

Individual marked	m 1	m 4	m 5	m 3	m 2	cr 1	Total frequency of subordinating
m 1	—	0	0	0	0	0	0
m 4	1	—	0	0	0	0	1
m 5	2	17	—	1	0	0	20
m 3	1	15	18	—	0	0	34
m 2	0	0	2	8	—	0	10
cr 1	0	0	0	0	2	—	2
Total frequency of dominance	4	32	20	9	2	0	

m 1-5; queen of *V. mandarinia*, cr 1: queen of *V. crabro*

five queens of *V. mandarinia* and a queen of *V. crabro* during the evening of May 1st in 1966 at a grove in Kibi. It is apparent that there is a linear dominance relationship among these queens. The order was as follows: m1 - m4 - m5 - m3 - m2 - cr1. As shown in Table 24, according to the order given above the individual which is next to the order could feed successively, and so forth, when an occupant had left the tree aperture. On May 1st the omega individual of *V. mandarinia*, m2, finished tree sap intake at 10:25 p.m. and then a queen of *V. crabro*, cr1, could finally occupy the tree aperture successively till 10:50 p.m.. On the following evening, May 2nd, I observed five queens of *V. mandarinia* at the same place, of which three, m5, m3 and m2, had been observed previous evening and held the same ranks among themselves. In the evening, a queen of *V. mandarinia* usually continued to take tree sap for about an hour. Then, with a full crop, she left the tree aperture, walked to the top of the tree and settled on the underside of a branch 7-8m high. Cleaning herself there, she fell asleep concealing the tips of her folded wings under the ventral surface of her abdomen, similar to the position found in hibernacula (MATSUURA 1966).

It is uncertain on what factors intra- and interspecific dominance relationship among queens of *Vespa* species is dependent. PARDI (1948) explained biologically that the dominance order among foundresses of *Polistes gallicus* was determined by the degree of ovarian development, and YOSHIKAWA et al. (1969) reported that the conditions of the reproductive system generally corresponded to the social order in a nest of *Paraschnogaster* sp.. In the case of *Vespa* queens visiting trees for sap it is difficult to find a correlation between social rank and ovarian development because the ovaries of queens are mostly undeveloped at the incipient stage of development during the feeding period soon after hibernation. It is suggested that the dominance interaction among *Vespa* queens, especially in *V. mandarinia*, results in a quantitative differences of food intake among them, and this may divide the post-hibernating queens into more or less distinct nutritional groups: a few high nutrition queens and the other low nutrition ones. It seems probable that such nutritional differences serve to differentiate the "quality" of queens, and it is pointed out that there exists a significant relationship between the quality of queen and the eventual size of the colony in the early stage of nesting in *Dolichovespula sylvestris* (BRIAN and BRIAN 1948, 1952) and in *Vespula vulgaris* (ARCHER 1980).

### 3) Inter specific relationships among workers at food sources

Interspecific dominance relationships among *Vespa* species is recognized not only among queens but among workers. The following order has been observed as an interspecific dominance relationship among five species of *Vespa* workers near Kibi: *mandarinia* - *anis* - *crabro* - *simillima* - *tropica*, which is the same as that found among the queens. The relations among all species, except for *V. mandarinia*, are sometimes indistinct in each encounter and may result in a severe combat with mandibles and stings.

*V. mandarinia* invariably occupies the first rank, monopolizes favourable sap sources, and expels other hornet species, beetles, butterflies, etc. If a tree sap site is occupied by *V. mandarinia*, workers of other species fly away with little hesitation soon after flying around the tree aperture. On the other hand, *V. tropica* is the mildest species and is often driven away by other species from a food source. In spite of their much larger body size, *V. tropica* queens are always expelled by a single *V. mandarinia* worker.

All the workers foraging at a food source always belong to the same colony although they cannot communicate the position of a source of tree sap to their nest mates. Workers from the same colony do not behave aggressively towards each other at a food source (Fig. 50). Other hornets of the same species belonging to alien nests are chased away by "legitimate" owners with or without combat whenever they try to approach the tree aperture. The defence of favourable tree sap sources is remarkable in *V. mandarinia*. The occupied food source is guarded by some individuals sitting around the tree apertures which do not return to their own nest. These behaviours indicate a well developed territorial defence.

Another peculiar habit at food sources is the frequent extranidal food regurgitation observed between *V. mandarinia* workers (OKADA 1961, MATSUURA 1975). Most vespine wasps are well known to transfer regurgitated food among workers (Montagner 1966, Spradbery 1973, Greene et al. 1976), but they generally do not interact with other foraging workers at most natural food sources. Food regurgitation between workers is confirmed within nests of all five *Vespa* species, but outside the nest. I have seen it occurring only once with two workers of *V. crabro* when visiting a tree sap source in 1974. In *V. mandarinia* the situation is





Fig. 50. *Vespa mandarinia* workers collecting sap exuding from the bark of an oak, *Quercus serrata*.



Fig. 51. Trophallaxis between two starved workers of *Vespa mandarinia* on the ground.

most frequently encountered among nest mates visiting the same tree sap sources, in which case the food flows unilaterally, not reciprocally. The more interesting instance is seen between two starved workers: embracing each other tightly and either lying or rolling on the ground or hanging from a tree branch by a single hind leg of one individual, they alternately beg and receive food (Fig. 51). The embrace lasts from several to tens of minutes and they do not easily separate even if disturbed. Such reciprocal trophallaxis is occasionally seen when this species attacks bee hives or nests of other social wasps, especially near the victim's nests during prolonged attacks, but so far is not confirmed within or near its own nests nor in



queens and males.

Food regurgitation among nest mates is apparently a habit independently acquired by various groups of social insects. The intense extranidal trophallaxis in *V. mandarinia* is certainly a specialized character. It must be mentioned that this phenomenon is mainly observed at sap sources and near victim's colonies, that is, at concentrated food sources. In honeybees, extranidal trophallaxis appears at artificial feeders but seldom at flowers. The habit in *V. mandarinia* may be related to its preference for such concentrated food sources.

## 5. Discussion

As is usual in other social insects, vespine wasps have evolved to be either highly specialized or very generalized in their food preference. In contrast to *Vespula* species with their small body size and omnivorous habit, *Vespa* species have an increased body size and predaceous habit, and have attained a co-existence in their feeding relationships by significant differences among them.

*V. tropica* is a typical specialist, being almost exclusively dependent on the brood of polistine wasps for its protein food, and the life cycle of this species is synchronized with that of polistine wasps.

On the other hand, *V. crabro* is regarded as a semispecialist, preferring various kinds of cicadas in Japan. It seems likely that this species is highly specialized behaviourally for capturing any cicadas, and they have an ability to utilize *Cryptotympana facialis*, which is about two times larger in body size than *V. crabro*, and hunting this largest cicada has so far been observed only by *V. crabro*. The hornets also have the ability to hunt a wide variety of insects when the preferred food source is lower in density. Rearing of sexuals in this species ceases in early September, in parallel with the disappearance of cicadas in southwest Japan. Such a feeding strategy makes better use of favourable food and contributes greatly to reduce the competition for the food resources among *Vespa* species.

Both *V. analis* and *V. simillima* have generalized their feeding considerably. It is plausible that these swift and agile species have the capacity to forage on various food sources scattered in the fields and these are found in large numbers in the regions where they build their nests. The contrasting features of the two species show that *V. analis* is small in colony size while *V. simillima* is much larger than any other *Vespa* species, and their peak populations occur at different times of the year, though both species have long-cycle characteristics. These differences may enable them to reduce competition for similar food resources.

On the other hand, *V. mandarinia* has achieved an efficient foraging strategy in that they attack in mass the colonies of other social wasps and honeybees, and also possess the ability to hunt a wide variety of large insects and spiders. A presumed course of evolution of this peculiar habit is briefly outlined below.

The large body size and enormously developed genae (MATSUURA and SAKAGAMI 1973), gave *V. mandarinia* the formidability to attack and to conquer other animals. By this ability, combined with an extraordinary aggressiveness and the strong toxic action of the stout sting, *V. mandarinia* occupies an unrivalled position among insects and other small animals, at least in Japan. In compensation, however, its relatively sluggish movement makes the capture of fugitive prey difficult which is especially conspicuous in comparison with some agile species such as *V. simillima* and *V. analis*. Consequently it is plausible that a slight displacement of the ecological niches has appeared between *V. mandarinia* and other congeneric species. *V. mandarinia* did not choose the specialized way to oligophagy as practiced by *V. tropica*. Keeping its polyphagous habit, *V. mandarinia* began to seek prey which was easy to catch. Among such prey there would be those making colonies, having a large amount of concentrated protein food. However the dependence on *Polistes* as in *V. tropica* was probably impossible for *V. mandarinia*, whose nests reach a large size and require a large quantity of animal diet. On the other hand, defense by nest owners presented no serious obstacle for *V. mandarinia*, and it was rather favourable for *V. mandarinia* if plenty of such self-defending individuals were available. The habit of attacking nests of other social wasps and bees would be a consequence of this tendency. Thus, *V. mandarinia* affects other congeneric species in two ways: as a competitor in seeking common food sources and as a predator. It is interesting that it does not hunt other species at tree sap sources, merely expelling them as lower ranked competitors. Attack on nests of other species, first started as individual hunting, would occasionally be rewarded by an

abundant supply of immatures to be foraged when the attack was continued to overcome the resistance of victims, even if accompanied by a loss of several to several tens of nest mates, which were transformed to meat pellets and fed back to the colony. The slaughter phase, the most interesting stage in the attack by *V. mandarinia* on other social insects, must be a later insertion between hunting and occupation phases. This phase is absent when attacking *Polistes* nests and seemingly not well developed when attacking *Vespula* nests, but it is distinct when attacks are made on victims with severe counter-attacks, i.e. other hornet species and *Apis mellifera*. Its releasing mechanism is still unknown but certainly is related to a change of motivation, which is probably released by the intense counter-attacks and the presence of nest mates. Its functional significance may be to facilitate the occupation of a victim's nest.

The defense of occupied nests against hornet invaders, recorded also in *V. orientalis* (ISHAY et al. 1967), is, in a lesser degree, recognized in the case of occupation of favourable tree sap sources, too. Such property defense is observed also in cleptobiotic stingless bees of the genus *Lestrimelitta* (NOGUEIRA-NETO 1970). Compared with the attack and nest occupation by this obligate robber bee, the attack by *V. mandarinia* is far less elaborate and efficient. From this fact, together with the maintenance of a polyphagous predaceous habit in general, the attack of *V. mandarinia* on nests of other social wasps, including both *Vespa* and *Vespula*, is interpreted as a retarded specialization. Up to the present, effective defense against *V. mandarinia* is known only in *Apis cerana*. This may be an adaptation acquired through a long contact with the powerful enemy.

The introduction of the European honeybee, *Apis mellifera*, into Japan in 1876 and subsequent development of modern apiculture offered a golden opportunity to *V. mandarinia*. The standard apicultural races of *A. mellifera* were confronted in Japan by a monstrous enemy, two times larger and incomparably more ferocious than *V. crabro* in their homeland. Solitary counter-attacks by bees, being effective for most enemies, served merely to increase the foraging efficiency of their enemy. For *V. mandarinia*, the European honeybee was certainly an ideal prey because of its large colony size and frequent counter-attacks as well as the feebleness of each individual. The outbreak of catastrophic damage by *V. mandarinia* is therefore regarded as a rare coincidence of ethological characters possessed by the prey and sought by the predator.

#### IV. DIVISION OF LABOUR

All the species of the genus *Vespa* in Japan found their colonies with a single fertilized queen. This solitary stage lasts for about two months from late spring to early summer until the emergence of the first worker. With the appearance of workers the labour of the queen varies in both quantity and quality in the course of colony development. Finally, she becomes restricted to oviposition, leaving nearly all the other duties to workers. Thus, the workers take charge of all the tasks in the colony except egg laying. However, when the queen is lost by accident or natural death in the course of colony development, one or more workers begin to lay eggs and produce some males (DARCHEN 1964, MATSUURA 1968). In this chapter the division of labour will be discussed on three aspects: behavioural differences between queens and workers, those during the adult lifetime of the workers, and those among workers in orphan colonies.

##### 1. Behavioural change of the queen in early nesting stage in relation to worker emergence.

The activities of the queen in solitary nest foundation are typical of a solitary wasp. After worker emergence, the colony undergoes a significant activity change to form the division of labour between queen and workers. The following information is mainly based on the data from a nest of *V. crabro* (C 6601), which was continuously observed from the solitary period to the cooperative period in 1966. Variations both in quality and in quantity of queen activities of *V. crabro* are shown in Tables 25, 26 and 27.

##### 1) Extranidal activities

- a) Collection of food; Food-collection activity consists of a linked sequence of searching, hunting, treatment of prey (=primary malaxation) and transport in the case of protein food; of searching, sucking and transport of carbohydrate food. The number of trips observed during the solitary period of *V. crabro* was 39, of which 30 trips were foraging for food and the time devoted occupied 46.0% on June 3rd, 1966 and

Table 25. Change in relative time spent in various activities by the queen of *Vespa crabro* during the observation period.

Date (1966)	Observation time	Total time of observation (min.)	Per cent of each time spent in			
			Extranidal activity	Resting	Intranidal activity Oviposition	Others
June 3	12:20-14:00	100	60.0	3.0	0.0	37.0
" 5	10:15-16:30	375	65.3	2.1	1.1	31.5
→ " 10	13:45-17:45	240	47.5	41.3	0.0	11.3
" 12	10:35-17:05	395	46.1	43.0	0.8	8.9
" 16	17:15-19:00	105	0.0	96.2	2.9	1.0
" 18	17:00-19:30	150	18.7	80.0	0.0	1.3
" 19	10:00-17:10	430	45.6	52.6	0.5	1.4
" 23	17:15-19:30	135	0.0	90.4	0.0	9.6
" 25	14:00-18:30	270	0.0	97.4	1.5	1.1
" 26	10:20-18:30	490	40.8	52.9	0.0	6.3
July 1	10:00-18:00	480	1.7	78.8	1.5	18.1
" 3	10:30-17:00	390	5.6	74.4	2.1	18.0
" 6	15:30-19:00	210	0.0	92.4	0.0	7.6
" 9	14:45-19:00	255	0.0	100.0	0.0	0.0
" 10	10:40-18:30	470	0.0	93.6	1.3	5.1
" 12	16:45-19:00	135	0.0	92.6	1.5	5.9
" 15	9:40-18:00	500	0.0	95.8	2.2	2.0
" 17	10:00-15:35	335	0.0	89.3	8.1	2.7
" 22	9:45-17:45	480	0.0	97.9	1.5	0.6
" 23	13:00-17:00	240	0.0	95.8	2.1	2.1
" 24	14:40-19:00	260	0.0	95.8	2.7	1.5
" 27	6:10-12:00	350	0.0	97.4	1.4	1.1

Arrow indicates the emergence of first workers.

55.9% on June 5th of the total observation time. Duration of a trip for carbohydrates is 5-16 minutes ( $\bar{m}=11.0$ , s.d.  $\pm 8.4$ ,  $n=23$ ) in the solitary period and 14-23 minutes ( $\bar{m}=16.3$ , s.d.  $\pm 3.4$ ,  $n=7$ ) on June 10th, when the first workers appeared. The last observation of foraging for food by the queen occurred on June 26th when only five workers were present. During the period from June 10th to 26th altogether 37 trips were observed, of which 36 were for carbohydrates and only one for insect prey. The time spent for foraging was 2-45 minutes ( $\bar{m}=18.2$ , s.d.  $\pm 10.4$ ) for a trip for carbohydrate and 27.5 minutes for insect prey. The intertrip time spent in the nest was 2-8 minutes ( $\bar{m}=4.3$ , s.d.  $\pm 2.0$ ) in the solitary period and 7-26 minutes ( $\bar{m}=12.3$ , s.d.  $\pm 14.1$ ) after the emergence of workers.

b) Collection of nest materials:

The time for gathering nest materials occupied 14.0% of the total time of observation on June 3rd and 9.4% on June 5th, respectively, in the solitary period. With the appearance of workers the queen gathered very few nest materials from the field (Table 26). The last collection of nest materials was observed on July 3rd, the final day of her field work. Thus, collection of nest materials by the queen continued for about three weeks after emergence of workers.

2) Intranidal activities

The proportion of inside tasks to outside ones by the queen increased with worker emergence: on June 3rd and 5th just before the emergence of workers it being 40.0% and 34.2%, respectively, of the observation time. On June 10th at the appearance of first workers, 52.5% of her time was spent in the nest though

Table 26. Change of foraging activities in *Vespa crabro* queen compared with those in workers.

Date (1966)	Foraging rate of queen (trips/hour observed)	Average time spent in the nest between foraging trips by queen (min.)	Total no. of trips recorded	Percentage ratio of various loads brought back in total trips recorded both in queen and workers										Total no. of foraging workers	
				Pulp		Liquid		Flesh		Water		No load			
				♀	♂	♀	♂	♀	♂	♀	♂	♀	♂		
June 3	4.20	5.7	7	—	37.1	—	42.9	—	0	—	0	—	0	—	—
" 5	4.96	4.3	31	—	35.5	—	64.5	—	0	—	0	—	0	—	—
→ " 10	1.75	18.0	7	0	0	0	100.0	0	0	0	0	0	0	0	0
" 12	1.22	36.6	8	23	0	0	100.0	69.6	0	0	0	0	0	30.4	2
" 18	0.40	122.0	1	23	0	4.4	0	69.6	100.0	26.1	0	0	0	0	3
" 19	2.09	13.6	15	38	0	26.3	93.3	29.0	0	18.4	0	0	6.7	26.3	4
" 25	0.90	—	0	24	0	4.2	0	34.2	0	12.5	0	0	0	29.2	3
" 26	0.86	28.6	7	35	0	28.6	100.0	31.4	0	5.7	0	0	0	39.3	4
July 1	0.13	?	1	92	0	20.7	0	43.5	0	14.1	0	0	309.0	21.7	3
" 3	0.46	123.3	3	68	100.0	10.3	0	79.4	0	5.9	0	0	0	4.4	3
" 6	0.00	—	0	56	0	16.1	50.0	30.4	0	30.4	0	0	0	3.6	8
" 9	0.00	—	0	36	0	5.6	0	83.3	0	0	0	0	0	11.1	9
" 10	0.00	—	0	129	0	7.0	0	84.5	0	5.4	0	0	0	3.1	8
" 12	0.00	—	0	30	0	16.7	0	60.0	0	6.7	0	0	0	16.7	6
" 15	0.00	—	0	81	0	21.0	0	37.0	0	25.9	0	1.2	0	14.8	5
" 17	0.00	—	0	40	0	30.0	0	45.0	0	12.5	0	0	0	32.5	4
" 22	0.00	—	0	88	0	18.2	0	37.5	0	8.0	0	29.6	0	6.8	4
" 23	0.00	—	0	64	0	6.3	0	31.3	0	4.7	0	46.9	0	10.9	7
" 24	0.00	—	0	113	0	29.2	0	46.0	0	7.1	0	12.4	0	5.3	11
" 27	0.00	—	0	100.0	0	28.0	0	39.0	0	25.0	0	2.0	0	6.0	8

The ratios in workers given by averages of individuals observed. Arrow indicates the emergence of first workers.

Table 27. Change of rate of various intranidal activities by the queen of *Vespa crabro*, per hour, during the observation period.

Date (1966)	Nest defence	Fanning	Nest cleaning	Spread of water	Food provision		Cannibalism	Enlargement of		Oviposition
					Liquid	Flesh		Envelope	Cell	
June 3	0	0	0	0	2.40	0	0	2.40	0	0
" 5	0	0	0	0	3.04	0	0	2.08	0	0.32
— " 10	0	0	0	0	1.75	0	0	0	0	0
" 12	0	0	0.15	0	1.37	0	0	0	0	0.15
" 16	0	0	0	0	0	0	0	0	1.71	0.57
" 18	0	0	0	0	0	0.80	0	0	0	0
" 19	0	0	0	0	2.23	0.28	0	0.14	0.42	0.14
" 25	0.22	0	0	0	0	0	0	0	0	0.44
" 26	0.12	0	0	0	0.86	0	0	0	0	0
July 1	0	0.25	0	0	0.99	1.25	0.12	0.38	0.25	0.38
" 3	0	0	0	0	2.77	0.77	0	0.92	0	0.93
" 6	0	0	0	0	1.14	0.57	0	0	0.29	0
" 9	0	0	0	0	0.24	0	0	0	0	0
" 10	0	0	0	0	0.26	0.26	0	0	0	0.38
" 12	0	0	0	0	0.44	0.44	0	0	0	0.44
" 15	0	0	0	0	0.12	0.12	0	0	0	0.60
" 17	0	0	0	0	0	0.18	0	0	0.36	0.98
" 22	0	0	0.12	0.12	0	0	0	0	1.38	0.38
" 23	0	0	0	0	0	0.25	0	0	0	0.50
" 24	0	0	0	0	0	0.23	0	0	0	0.69
" 27	0	0	0	0	0	0.17	0	0	0	0.34

Arrow indicates the emergence of first workers.

newly emerged workers had not yet started "social" activities. The queen continued occasional intranidal activities as she did in the solitary period until the last observation of July 27th, though she came to spend most of her time resting on the comb (Table 27). Detailed procedures for various activities are described as follows.

#### a) Provisioning of larvae

The food of larvae in *Vespa* is of two types, liquid and solid. Immature larvae, 1st to 3rd instars, are fed only on liquids. On the other hand, 4th and 5th instar larvae, except for those of *V. tropica*, are provisioned with both liquid and solid. In the case of solid foods, a queen, having finished malaxation, approaches a group of larvae carrying the flesh pellet with her mandibles. From the front of the pellet a small morsel is cut off and placed on the larval mouthparts. This procedure is repeated until the entire pellet has been disposed of. A single pellet is distributed to 3–7 mature larvae. After worker emergence a part of the prey captured by the queen is frequently shared among workers as soon as she returns to the nest. The queen may obtain a food pellet from a foraging worker or a malaxating one on the comb. Once the queen begins to feed the pellet to larvae, she never shares the pellet with workers. Having finished provisioning the larvae, she usually performs a cleaning behaviour with her legs and mandibles. Then she begins again to approach the larvae and to feed liquid, sucked from the prey during malaxation, to the larvae in such a manner that she gets the tongue near to the mouthparts of the larva. In the case of liquid food containing carbohydrates, she first cleans the legs and antennae soon after the foraging trip. Then, she begins to provision in a similar way. The queen continues provisioning the larvae with food after cessation of her foraging activity though the frequency becomes very low. The last distribution of liquid carbohydrates by the queen was observed on July 27th, seven weeks after worker emergence. Malaxation and food provisioning occupied 17.0% and 19.4%, respectively, of her time on June 3rd and 5th of the solitary period and 0.0–15.4% during the period after worker emergence in each daytime observation.

MOKIMOTO (1960) suggested that for *Polistes chinensis* the feeding behaviour of the queen is released by certain stimuli emitted by larvae. In all *Vespa* species the 5th instar larvae scratch the walls of their cells with their mandibles when they require food, and this performance apparently serves to attract adult nurses. In *V. tropica* the queen taps with the mid- and hind legs on the comb for a while when she returns to the nest with food in her crop. This is regarded as a signal system in feeding activity between adults and larvae.

#### b) Nest construction

Building activities inside the nest include such diverse operations as converting raw materials into pulp, making the pedicel and painting a lustrous substance on its surface, making cells and lengthening their walls, making and enlarging the envelope and putting paste on cocoons. These tasks are chiefly accomplished with her mandibles and fore legs. Materials for nest building are gathered not only from the field but from within the nest. The queen frequently scrapes the bottom part of the envelope or the upper edge of a cell and incorporates the material again into the nest structure. Without gathering the material, she sometimes rethins still moist parts of cells and envelope recently elaborated by workers.

The queen of *V. crabro* spent, 20.6% and 12.6% of her time in enlarging the envelope in the solitary period on June 3rd and 5th, respectively. With the appearance of workers the time spent in nest building, in such activities as coating the pedicel, lengthening cell walls and enlargement of envelope, decreased to 4.6% of her time observed and cell initiation was never been observed after worker emergence. Retirement from building activities advances through four steps in which the following processes are successively eliminated. (1) Initiation of cells, (2) Enlargement of cells and envelope with nest materials which she herself has collected from the field, (3) Enlargement of cell walls with nest materials collected by herself within the nest, (4) Re-enlargement of cell walls without nest materials. This behaviour continued for a fairly long time after the emergence of workers. I observed the queen rethinning a moist part of a peripheral cell in a different nest of *V. crabro* with about 150 workers on August 15th, 1965.

In all *Vespa* species the nest material collected by a queen or worker is always processed by the collector herself over a whole procedure, and is used for one purpose, as also exhibited in *Polistes* wasps (WEST-EMERHARD 1969).



c) Nest preservation

This includes such tasks as nest cleaning, nest defence and regulation of nest temperature, these mostly being made less intensely than by workers. Behaviours for nest preservation by the queen of *V. crabro* are rare after worker emergence as well as in the solitary period. The following behaviours were observed once in each case. (1) Coating the pedicel (June 16th), (2) Removal of the fragments of the cap of a cocoon which had been cut away by an emerging worker (June 26th), (3) Fanning (July 1st), (4) Regurgitating the water on the caps of cocoons (July 22nd). These disappear with the increase in number of workers, eventually being left entirely to the workers.

d) Oviposition

In all *Vespa* species the oviposition process consists of a linked sequence of: pre-fixation (cell inspection

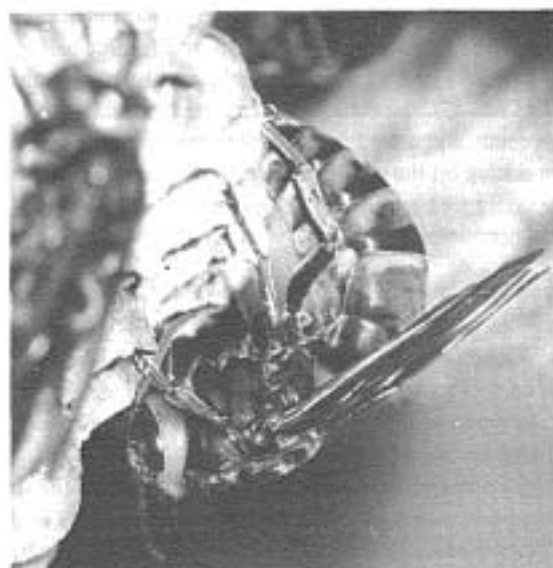


Fig. 52. Oviposition by a *Vespa crabro* queen.



Fig. 53. Egg-laying workers of *Vespa crabro* in an orphan colony. Three of them are inspecting the eggs deposited.



and insertion), fixation, oviposition, self-cleaning, abdomen withdrawal and food intake (almost entirely larval secretion). The duration of oviposition from the fixation to the extraction of the body ranged from 82–82 seconds ( $\bar{m}=136.7$ ,  $n=16$ ) for *V. crabro* queens. (Fig. 52). On the other hand, in the case of worker oviposition in the same species, the layer stays at the cell for a while after oviposition and continues to inspect the egg deposited (Fig. 53). The oviposition rate of a *V. crabro* queen did not reach 1.0 egg per hour through the observation period even after worker emergence. The number of eggs laid per day was 0–5 eggs in the solitary period and an average of 4.8 eggs (max. 14, July 24th) for 49 days after the emergence of the first workers. The shortest pause between successive ovipositions was 20 minutes on June 25th. On the other hand, when the worker number reached over one hundred, the number of ovipositions increased rapidly, probably reaching more than several tens per day.

#### e) Resting

The most remarkable feature after the emergence of workers is that the queen comes to spend most of her time at rest on the comb, with only occasional cell patrols and trophallaxis with workers and larvae. The queen of *V. crabro* spent only 3.0% and 2.1% of the total time of observation resting on the comb on two days of the solitary period (Table 25), respectively. After June 10th when the workers emerged she was frequently seen resting on the comb, and after July 6th when she stopped foraging activities, most of her time, 89.3–97.9%, was spent in resting on the comb. However, after early August, the resting time of the queen seems to decrease to some extent with a corresponding increase in the number of cells ready for egg laying as the number of workers increases.

## 2. Relations between labour and age in workers

### 1) Emergence of workers

Workers emerge from the pupa inside the cocoon and spend 6–10 hours in their cells in order that the wings and integument can harden before they emerge from the cells. At the time of emergence they secrete salivary fluid which helps to moisten the cell cap and to make egress easier. Then, they gnaw the cocoon cap with their mandibles from the inside and cut a ragged hole toward one side of the end of the cocoon. It takes about 30–40 minutes from the beginning of cocoon gnawing to the time when they get out from the cell. During the whole process they get no help from the older workers in the nest. On the other hand, when *Bombus* species workers emerge, they are helped out of their cocoons by several workers in the nest (KATAYAMA 1966).

### 2) Behaviours of workers soon after emergence

Newly emerged workers immediately seek out full grown larvae and receive salivary secretion for their first food as an adult. They do not trim the ragged edges of the cell which they have just left but leave this task for the older workers. They move very little and spend most of their time thrusting their head and abdomen into empty or egg cells at the centre of the comb except for occasional food intake from larval secretion, self-cleaning and slow walking on the comb for the first day of their adult life. This applies in all five *Vespa* species (Tables 28, 29, Figs. 54–56)

Intranidal activities are very rare for the first day. A few exceptions have been observed in a nest of *V. crabro* (C6601) in the early nesting stage. In this nest the following behaviours were observed by seven workers once in each case: (1) Re-enlargement of the cell wall without nest materials (three workers), (2) Enlargement of the cell wall with nest materials collected by herself within the nest (one worker), (3) Enlargement of the envelope with nest materials collected by herself within the nest (one worker), (4) Malaxation of prey with provisioning to larvae (one worker), (5) Cleaning a foraging worker soaked with rain in the field (one worker).

As early as their second day they begin to engage in a variety of intranidal activities, such as cell initiation, cell enlargement, provisioning brood and thermoregulation etc., though they are able to be distinguished from older workers by their body colour. Some of them make their first flight at 2 days old, as soon as they are endowed with flying ability.

### 3) Orientation flight and foraging trips

Table 28. Per cent of time spent in each activity of a single *Vespa similis* worker (No.9) during its lifetime.

Activity	Age in days														
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<b>Extranidal act.</b>															
Orientation	—	—	0.8	0.1	—	—	—	—	—	—	—	—	—	—	—
Pulp collection	—	—	—	—	1.3	2.9	5.7	—	13.2	10.9	6.2	10.2	5.3	3.1	10.8
Food collection	—	—	—	1.6	2.1	4.3	18.4	44.4	19.2	15.1	6.8	21.2	28.8	7.5	15.1
Water collection	—	—	—	—	0.8	2.1	8.3	—	11.4	3.2	5.1	9.5	3.9	1.5	4.5
No load collec.	—	—	—	19.7	2.9	0.7	7.9	1.1	1.5	1.1	0.1	0.3	2.8	0.2	0.3
<b>Intranidal act.</b>															
Pulp malaxation	—	—	0.6	1.5	1.3	2.2	1.3	—	6.4	1.5	2.3	2.8	1.1	1.3	2.8
Scraping envelope	—	—	3.4	5.2	9.1	3.3	1.6	—	1.7	1.3	2.1	1.1	2.3	3.5	3.5
Enlarging enve.	—	—	0.4	4.6	6.9	—	6.2	—	0.8	2.9	4.2	10.1	7.4	3.1	8.1
Making cell	—	3.1	3.3	5.1	11.1	23.2	6.3	—	1.5	3.2	3.5	5.9	3.8	1.1	3.4
Making pedicel	—	1.7	—	—	—	—	—	—	0.1	0.2	1.0	0.3	0.5	0.2	0.2
Feeding larvae	—	4.1	1.5	2.8	0.1	—	1.5	1.2	1.2	2.2	2.2	1.8	2.1	3.1	3.1
Prey malaxation	—	0.6	—	0.7	0.8	—	—	—	3.2	0.9	1.5	2.1	1.6	0.9	0.5
Food exchange between adults	—	0.1	0.2	0.5	1.6	0.5	0.3	0.4	1.0	0.5	1.8	1.5	0.8	0.8	0.7
Food intake from larvae	2.4	5.3	0.3	0.4	0.6	0.6	1.7	—	0.3	0.8	0.9	1.9	0.8	1.1	0.9
Body cleaning	3.0	—	3.9	5.0	7.4	—	3.5	9.4	0.5	1.8	2.3	5.2	3.9	3.1	6.2
Nest cleaning	—	—	—	1.3	—	—	4.9	2.2	4.1	1.2	4.1	0.3	1.1	3.1	1.1
Spitting water	—	—	11.7	0.8	—	3.4	2.5	—	4.0	1.5	1.8	3.2	1.1	0.8	1.3
Fanning	—	0.0	0.3	0.1	0.8	—	4.6	—	1.5	0.4	5.5	0.8	0.5	3.5	5.1
Resting with occasional cell patrol	94.6	85.1	73.6	50.6	52.4	56.8	25.3	41.4	28.4	51.3	48.6	21.8	32.2	62.1	32.4
Duration of obs. (hours)	4	4	5	9	5	3	9	3	2.5	5	8.5	3	5	8	4

Disappearance from the nest

The first flight was observed at 2 to 4 days old in 247 individually marked workers of the five *Vespa* species (Table 30). When a worker first leaves the nest she makes two or three orientation flights during the course of which she learns the position of the nest entrance relative to neighbouring objects. The worker first flies straight out of the nest for about 20–30cm, then turns to face the entrance, flying slowly with to-and-fro movement. Still facing the entrance she extends gradually the distance from the nest to some 3–5 metres, and then abruptly returns to the nest. The second flight is usually carried out on the same day in a similar manner to the first, but the distance from the nest is extended to 15–20 metres. This may give the worker sufficient information though some require a third orientation flight. The first orientation flight took for about 70–100 sec. and the second decreased to 130–150 sec. in many *Vespa* workers.

The first foraging trip is performed after the second or third orientation flight. During this trip the young worker collects all types of loads, such as nest materials, water, liquid food and prey, in a similar way to older ones in the field.

#### 4) Activities of marked workers during their adult life

The activities of each of the marked workers of the five species, during their adult life are summarized in Tables 28, 29, Figs. 54–56. These results indicate that the workers of *Vespa* take an active part in the affairs of the colony very soon after emergence. They began to perform a variety of intranidal activities—brood care, nest construction and nest preservation—as early as their second day. They foraged after only

a few days. Thereafter, both extranidal and intranidal activities were found in workers of all age ranges and all of the workers daily performed foraging activities until their last day alive. Judging from these results, together with more observations on other individuals, it is certain that a division of labour based upon age difference is not established in *Vespa* workers, unlike some *Vespa* workers in which there is some correlation with their age (EDWARDS 1980 from POTTER 1964).

Another important feature in the proportioning of time spent in various kinds of activity is that *Vespa* workers spent about one half of their time during the day resting with or without slow walking on the comb. These unproductive activities are regarded as providing a stand-by work force which can be recruited whenever conditions change and the colony needs to meet a new situation.

Similar results have been obtained in *Apis mellifera* workers, which spend about two-thirds of their time either resting or wandering through the interior of the nest, an activity that LINDAUER (1952) refers to as patrolling. He explained that these two outwardly unproductive activities enhanced the capacity of the colony as a whole to respond to capricious changes in the environment. This account could be applied to the *Vespa* workers too, and the daily life of workers is in general a repetition of the cycle consisting of resting, patrolling and performance of tasks as stated for the honeybee (SEKIGUCHI and SAKAGAMI 1966).

Table 29. Per cent of time spent in each activity of a single *Vespa analis* worker (No.4) during its lifetime.

Activity	Age in days																
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Extranidal act.																	
Orientation	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pulp collection	—	—	—	1.2	7.5	6.6	10.6	9.5	3.4	4.5	6.8	5.2	6.0	3.5	7.2	5.5	—
Food collection	—	—	—	3.1	9.3	5.9	5.8	16.2	11.2	5.3	14.3	7.3	11.0	4.9	7.8	5.8	—
Water collection	—	—	—	1.2	1.1	1.2	0.2	0.5	1.0	—	—	1.1	0.2	—	—	1.0	—
No load collec.	—	—	—	3.5	1.4	3.4	5.4	3.5	3.5	2.1	5.5	2.4	5.7	3.1	2.5	3.0	—
Intranidal act.																	
Pulp malaxation	—	—	1.2	2.4	3.2	4.5	8.3	7.8	2.5	6.0	7.5	6.2	7.2	4.5	9.5	6.2	Disappearance from the nest
Scraping envelope	—	1.2	4.1	3.1	2.1	0.5	1.5	2.5	1.5	0.2	2.1	1.5	1.1	0.3	3.4	2.5	
Enlarging enve.	—	—	2.2	6.2	6.5	7.2	12.1	11.1	4.0	7.5	10.2	7.4	7.8	5.3	10.2	8.0	
Making cell	—	4.2	2.4	3.8	2.1	1.5	1.1	2.8	2.2	0.1	0.5	1.8	1.2	0.5	2.9	1.5	
Making pedicel	—	—	0.1	0.2	0.1	—	0.3	0.2	0.1	—	—	0.1	—	—	0.2	0.1	
Feeding larvae	—	5.5	3.1	5.9	3.7	6.1	4.1	3.3	2.1	4.4	5.8	3.3	2.5	3.1	6.0	5.2	
Prey malaxation	—	2.1	2.8	5.1	4.5	5.1	7.5	10.1	13.3	5.9	10.2	4.9	5.9	6.2	4.9	4.8	
Food exchange between adults	0.2	1.2	2.2	2.2	3.2	1.5	2.2	2.9	1.6	0.5	0.6	0.8	1.2	2.4	2.6	0.9	
Food intake from larvae	3.1	6.2	3.1	1.8	2.5	2.0	3.5	2.1	1.5	0.5	1.1	1.3	2.1	1.5	3.2	1.1	
Body cleaning	5.2	1.1	0.5	0.3	0.2	1.0	0.5	0.6	0.3	1.0	0.5	0.3	0.5	0.3	0.3	0.6	
Nest cleaning	—	1.1	0.3	1.3	2.2	0.5	0.6	0.4	0.4	1.1	0.2	0.4	0.1	1.1	1.2	0.5	
Spitting water	—	—	0.2	0.3	0.5	0.6	0.5	0.3	0.2	0.2	0.1	0.1	0.3	0.3	0.5	0.5	
Fanning	—	0.2	0.3	0.3	0.2	0.2	0.3	0.2	0.3	0.4	0.1	0.3	0.5	0.4	0.6	0.4	
Resting with occasional cell patrol	99.5	77.2	77.3	64.2	49.7	52.2	35.5	26.0	50.9	60.3	34.5	55.7	46.7	62.6	37.0	52.4	
Duration of obs. (hours)	3	3	3.5	4	2.5	8.5	9	4	3	4	3	8	9	4	4	5	

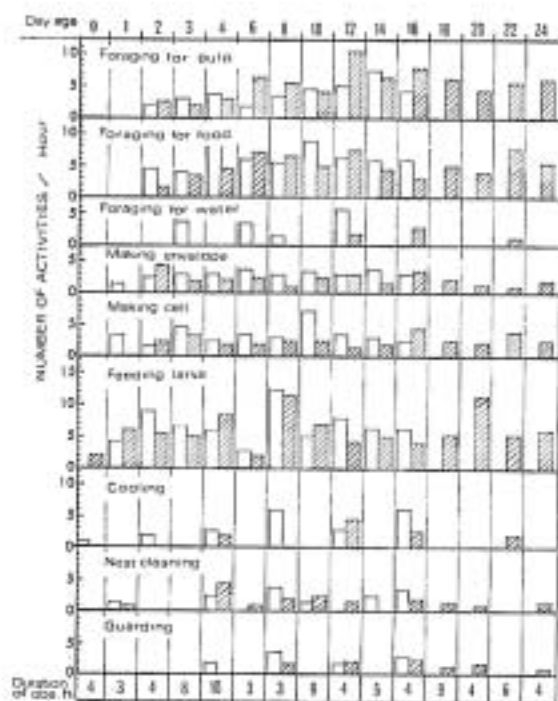


Fig. 54. Activities of two marked workers (No. 38: □; No. 41: ▨) of *Vespa crabro* during their lifetime (No. 38: 17 days; No. 41: 25 days).

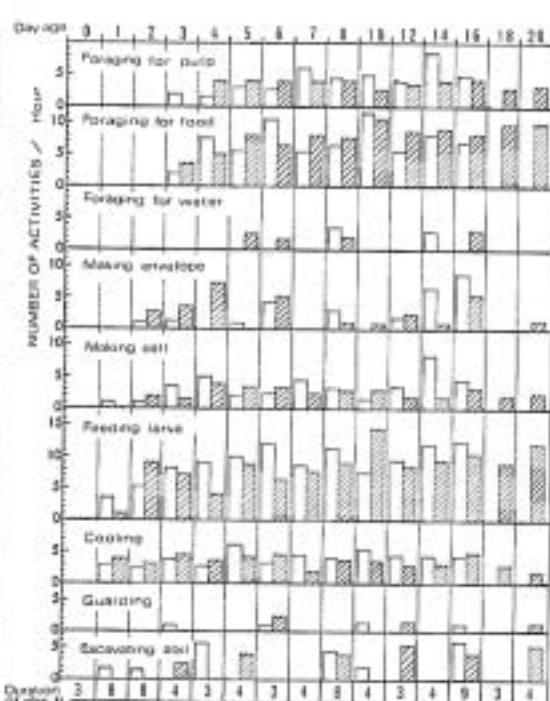


Fig. 55. Activities of two marked workers (No. 5: □; No. 6: ▨) of *Vespa mandarinia* during their lifetime (No. 5: 18 days; No. 6: 22 days).

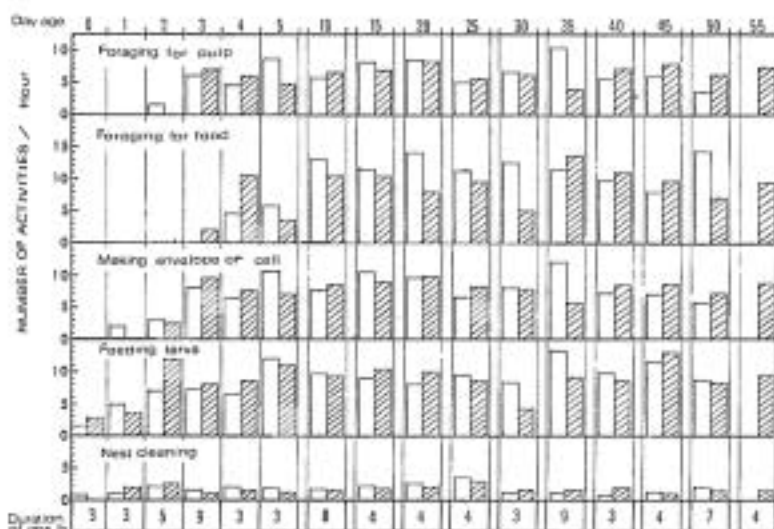


Fig. 56. Activities of two marked workers (No. 2: □; No. 3: ▨) of *Vespa tropica* during their lifetime (No. 2: 53 days; No. 3: 61 days).



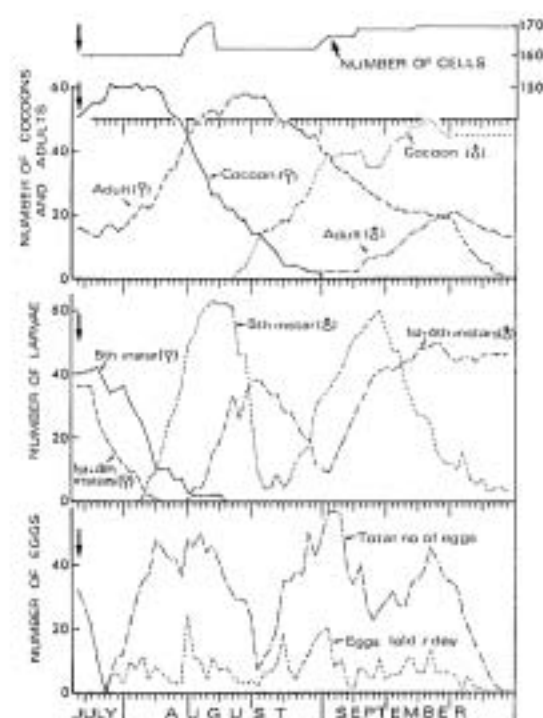


Fig. 57. Change in composition of brood and adult populations in an orphan colony of *Vespa analis* (A6705) after the death of the queen. Arrow indicates the death of the queen.

Fig. 57 shows the fluctuations in the number of workers, cells and of nest contents during the period from removing the queen to the disappearance of the last workers. The maximum number of workers reached 58 on August 19th, and thereafter decreased. The immature stages under the queenright condition all reached the adult stage and all of them emerged as workers. The rate of worker emergence was 2.1 individuals per day on average, during the period from July 26th to September 4th, when the last worker emerged. On the other hand, the males emerged from September 1st and thereafter continued to emerge even after the disappearance of workers. It is assumed that all these males were produced from eggs laid down by worker No. 1.

The rates of cell construction in the colony were considerably lower than those in queenright colonies throughout the observation period (Fig. 57). The total number of cells constructed after death of the queen was only 17, and 8 old cells were destroyed by workers. At the last observation on September 30th, the nest consisted of two combs with 169 cells.

## 2) Division of labour among workers

Table 31 gives the individual differences in function among 10 marked workers which remained in the nest after the death of the queen. As stated in the previous section, worker No. 1 became very aggressive and was always dominant in her interactions with the other workers. She frequently solicited from other workers aggressively with mouthparts. This worker stopped her extranidal activity on the death of the queen and specialized in oviposition, i.e., she became the sole egg-layer among the workers of the colony. All 49 examples of oviposition observed were exclusively done by worker No.1. Judging from Fig. 57 and Table 31, worker No. 1 oviposited 0.73 eggs per hour of observation and it is estimated that a total of



408 eggs were laid in 61 days, an average of 6.7 eggs per day (maximum: 24 eggs on August 24th). Worker No.1 continued also to malaxate prey for provisioning to the larvae as long as she lived.

All the marked workers except for worker No.1, engaged in all extranidal activities during the observation period. Activities inside the nest other than oviposition, such as nest construction, brood care and nest preservation, were shared by all workers in the colony including worker No.1.

### 3) Characteristics of laying workers

The laying worker No.1 in the colony became easily distinguishable from the other workers on the basis of her external features, being characterized by the loss of body hairs resulting in a black shining body. These external features of the laying worker in an orphaned colony show a marked resemblance to the queen in populous colonies of the same species after August (MATSUURA 1968, 1974), and this "substitution queen" was frequently observed in orphan nests of the same species taken from early August to early November (Tables 32 and 33).

In these substitution queens the loss of body hairs was conspicuous on the gena and mandibular base, and on the thorax and abdomen, as reported in *V. simillima* by YAMANE (1974).

There are some distinct differences with regard to the ovarian development of the workers between queenright and queenless colonies. In the queenright colonies the majority of workers had undeveloped ovarioles with incipient constrictions or with distinct constrictions marking the appearance of oocytes (Fig. 58), except one of the workers which possessed developed ovaries with mature oocytes in colony A 7521 collected at the end of the season. On the other hand, in queenless colonies, the proportion of workers with a number of mature oocytes as well as successively developing ones (Fig. 58 and Table 33) was very much higher compared to that of workers in queenright colonies, and some of them possessed ovaries with fully matured oocytes not very different from that of queens (Fig. 58). In an analysis of ovarioles, the largest queen oocyte was 3.4mm long and the largest worker one was 3.3mm long, and the number of ovarioles was 7/7 (left/right) in queens ( $n=12$ ) and 6/7 or 7/7 in workers ( $n=35$ ). Furthermore, the

Table 32. Ovarian development of *Vespa analis* workers in queen-right colonies.

Nest code	Date	No. of workers in each stage of ovarian development*				Total no. of adult hornets				No. of cells
		I	II	III	IV	♂	♀	♀	♂	
A6705	Jul.23'67	12	5	0	0	1	17	0	0	162
A7207	Jul.30'72	10	4	0	0	1	14	0	0	108
A7510	Aug.14'75	12	28	1	0	1	41	0	0	223
A7513	Aug.20'75	75	67	0	0	1	142	0	0	510
A6709	Aug.24'67	22	18	0	0	1	40	0	0	225
A6711	Sep. 2'67	32	23	0	0	1	55	0	0	200
A7404	Sep. 2'74	18	37	0	0	1	55	0	0	230
A6712	Sep. 4'67	35	65	0	0	1	100	0	0	316
A7211	Sep.10'72	48	40	0	0	1	88	0	0	333
A7212	Sep.13'72	32	27	0	0	1	59	0	0	204
A7406	Sep.20'74	27	25	1	0	1	53	9	1	244
A7310	Sep.23'73	32	20	1	0	1	53	6	27	463
A7312	Sep.23'73	43	40	0	0	1	83	3	41	538
A6820	Sep.24'68	33	26	1	0	1	60	10	0	377
A7313	Sep.24'73	7	13	1	0	1	21	8	4	225
A7108	Sep.25'71	63	45	2	0	1	110	8	24	553
A7517	Sep.27'75	49	41	0	0	1	90	0	34	531
A6821	Oct. 6'68	48	77	1	0	1	126	0	30	736
A7521	Oct. 7'75	10	26	1	1	1	38	0	25	428
A7215	Oct.10'72	10	28	1	0	1	39	1	58	549
A7110	Oct.18'71	9	20	3	0	1	32	1	36	369

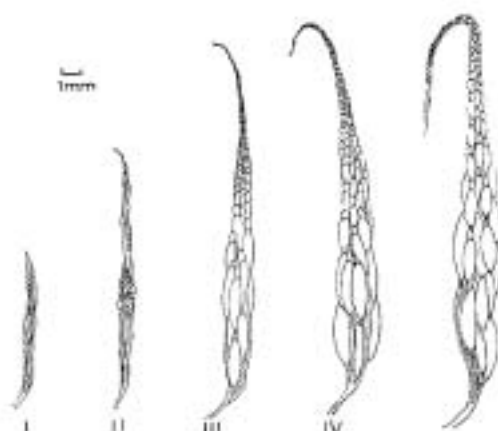
\* See Fig. 58

Table 33. Ovarian development of *Vespa analis* workers in queenless colonies.

Nest code	Date	No. of workers in each stage of ovarian development*				Total no. of adult hornets			No. of cells
		I	II	III	IV	♂ **	♀	♂	
A7509	Aug. 1'75	21	2	2	2	27(0)	0	20	242
A6706	Aug. 17'67	8	69	38	19	134(0)	0	13	463
A7309	Aug. 20'73	23	42	20	3	88(1)	0	4	452
A7511	Aug. 20'75	4	2	1	1	8(0)	0	0	51
A7512	Aug. 20'75	1	3	4	4	13(0)	0	0	120
A7308	Sep. 12'73	3	32	37	3	75(1)	0	41	359
A7311	Sep. 23'73	3	12	28	2	45(1)	29	7	356
A7516	Sep. 26'75	8	21	0	1	30(0)	0	58	229
A7314	Oct. 1'73	12	12	23	6	53(1)	0	61	490
A7213	Oct. 6'72	3	9	34	15	61(1)	24	63	714
A7517	Oct. 7'75	10	25	5	14	54(0)	5	84	699
A6904	Oct. 10'69	5	30	38	12	85(1)	2	77	702
A7216	Oct. 12'72	0	3	2	3	8(0)	0	82	602
A6717	Oct. 14'67	5	13	19	2	39(0)	0	32	412
A7111	Oct. 19'71	4	3	16	1	24(0)	77	6	707
A7315	Oct. 25'73	0	5	10	3	18(0)	4	19	323
A7522	Oct. 29'75	0	0	0	1	1(0)	0	15	752
A6827	Nov. 1'68	0	3	3	1	7(1)	0	11	689
A7114	Nov. 4'71	1	7	24	1	33(1)	1	0	675
A6905	Nov. 8'69	5	24	29	2	60(0)	65	0	467

\* See Fig. 58

\*\* Value in parentheses is the number of substitute queens.

Fig. 58. Ovaries in *Vespa analis* worker (I-IV) and queen (right): I-II; undeveloped, III; rather developed, IV; developed, following loss of queen.

number of fully matured oocytes was 8 to 13 in queens ( $n=13$ ) and 7 to 14 in workers ( $n=35$ ). These data indicate that there are few differences in the size and volume of ovaries between queens and workers.

In the queenless colonies, however, it is not clear whether all the workers with fully matured ovarioles could lay eggs or not, because the substitution queen in the colony A6705 was the only individual observed ovipositing, and the number of substitution queens was always one in the other queenless colonies in the same species (Table 33).

In addition to the external features, the substitution queen is characterized by a remarkable prolongation of its life span, compared with that of workers in the same colony. In colony A6705 the substitution queen died on September 28th, thus she survived for as much as 67 days after the death of the founding

Table 34. Longevities of *Vespa analis* workers in an orphan colony (A6705).

	Life span (in days)	No. of indi. obser.	Time of death
Worker No. 1 (substitute queen)*	> 67	1	Sep. 28th '67
Workers, not laying**	$\bar{m} = 22.3 \pm s.d. 18.5$ , Range: 3- 45	41	From July 25th to Sep. 19th

\* Date of emergence is uncertain.

\*\* These emerged from late July to early August.

queen. The longevity was about three times as long as the mean longevity of the workers which emerged from late June to early August in the same colony (Table 34).

#### 4. Discussion

##### 1) Behavioural change of queen in early nesting stage

One of the most characteristic features in the social insects is the functional division of labour between reproductives and non-reproductives. The vespine wasps are generally considered as representing the most advanced stage of social wasps, exhibiting a marked differentiation of two female castes, the queen a larger and almost exclusively egg-laying female, and workers -smaller, sterile females and exclusively haplometrotic nest foundation (at least in so far studied temperate species). Throughout the solitary period, the queen behaves as if she were a solitary wasp. With the emergence of workers, her behaviour varies in both quantity and quality in the course of colony development.

In the vespine wasps, VERLAINE (1932) has observed in *Dolichovespula media* that the queen would continue to forage and build a nest two months after the emergence of the first worker, but in this colony the number of adults was only twelve. BRIAN and BRIAN (1952) reported slackening of queen foraging of *Dolichovespula sylvestris* soon after the workers started foraging, although it is quite possible that she had reduced her outdoor activity earlier; she was not seen to go out after the 33rd day, but one queen, which produced only three workers frequently left the nest as late as the 50th day and this change is probably related in some way to the presence of foraging workers. In *Vespula germanica* and *V. vulgaris* with populous colonies, SPRADBERY (1965) stated the cessation of extraovipositional duties by the queen when four or more workers were present. SHIDA (1959) observed in *Vespula flaviceps* that the queen had ceased to leave the nest with 11 workers on June 11th. As to *Vespa* species, ISHAY (1964) reported on *V. orientalis* that the workers aided the queen in nest construction and larval nursing between mid-May and mid-June in Israel, and the queen, then, principally occupied herself in oviposition without going out. In *V. analis*, a queen stopped her extranidal activities when six workers were present in early July though she still continued some intranidal activities (MATSUURA 1974).

The previous reports have dealt almost exclusively with foraging behaviour of the queen. Little attention has so far been paid to intranidal activities of the queen in the early nesting stages. Even after the queen of *Vespa* ceases to leave a nest, she continues to engage in inside work, i.e. cell enlargement, provision of malaxated prey and liquid to the larvae and thermoregulation, for about a month. Thus, the cooperative nesting stage between queen and workers lasts for about 50 days after the emergence of the first worker in the nest of *V. crabro*. On the other hand, in *Vespa tropica*, which has the smallest colony size among the *Vespa* species in Japan, generally similar to that of the Japanese *Polistes* in colony size (MATSUURA 1970), the queen participates in intranidal activities not only soon after emergence of workers but throughout her life (MATSUURA 1974). These facts suggest a possible correlation between colony size and gradual change of queen activities in *Vespa* species in such a way that the larger the typical colony size of a species, the earlier this occurs, though such change is obviously related in some way to the presence of workers, especially foragers.

In polistine wasps the tasks of colony-building and brood care are shared by the foundress and workers, though the former is usually the sole egg-layer and she has at least four distinctive behavioural characteristics: egg-laying, superior dominance, cell initiation, and specialization in pulp foraging (West-Eberhard 1969). West-Eberhard pointed out that cell initiation and pulp foraging by the foundress of *Polistes* are characteristics directly associated with developed ovaries or dominance as shown by the experiments of PARDI (1948). In *Polistes huntleri*, the foundress takes a mass of pulp from a returning worker to construct new cells at the edge of the comb (MICHENER and MICHENER 1951).

On the other hand, no *Vespa* queens engage in cell initiation after worker emergence, even in *V. tropica*. The abandonment of cell initiation by the queen is probably correlated with larger colony size. Even in the cooperative period, the mode of life in *Vespa* is regarded as more differentiated than in polistine wasps. Furthermore this period may reflect a primitive polyethism between queen and workers in the earlier stage of social evolution passed through by *Vespa* species.

## 2) Relations between labour and age in workers

Age-conditioned polyethism has been recognized among the workers in a colony of the honeybee (RÖSCH 1925) and ants (SUDD 1967). In social wasps, polyethism according to age is weakly defined. *Polistes jadwigae* workers do not forage until about a week following emergence and the older workers have a greater tendency to participate in domestic work, but there is otherwise no clear scheduling of tasks (YOSHIKAWA 1963). In *Vespula* species, SHIDA (1959) reported in *V. flaviceps* that collecting nest materials was chiefly performed by older workers. According to MONTAGNER (1967), *Vespula* workers assist in nest building during the first few days after emergence, and then they also begin to feed larvae; finally, some individuals add foraging to their repertory. BRIAN and BRIAN (1952) stated that the workers of *Dolichovespula sylvestris* assisted in the malaxation of flies brought in by other workers very soon after emergence and foraged only a few days after emergence. GAUL (1948) found in his observations on some colonies of *Vespula* and *Dolichovespula* that no age distinction existed which might predetermine the occupation of any worker. In the case of *Vespa*, a similar pattern has been recognized and the workers take an active part in various tasks of the colony very soon after emergence.

On the other hand, in the workers of the honeybee, *Apis mellifera*, some activities depend on particular physiological conditions which are age-conditioned; for instance, food discharge from the hypopharyngeal glands and wax secretion on wax glands, etc. (KING 1933). In *Vespa* species it is likely that the workers have no schedules for nursing and nest construction which are limited by glandular activity as is known in the honeybee. Therefore, it appears that *Vespa* workers can perform any tasks a few days after emergence.

## 3) Division of labour in an orphaned colony

In the course of colony development a considerable number of colonies lose their queens by accident or natural death after the emergence of workers. Nevertheless, most of these orphan colonies survive for more than a few months and frequently contribute to male production.

MARCIAL (1896) first reported in his studies on *Vespula* spp. that workers developed their ovaries soon after removing the queen, and some of them began ovipositing within 10 days. In *Vespa* also, it is observed that workers oviposited several days after the queen's death (ISHAY et al. 1965, MATSUURA 1968). These cases indicate that some workers of vespine species have the potential ability to oviposit in the orphaned condition in spite of their differences in morphological and physiological factors (TAKAMATSU 1952, BLACKITH 1958, SPRADDER 1965). In the case of *V. analis* it is recognized that such laying workers are different from the other workers in orphaned colonies and are characterized by the following points: (1) the primary or sole egg-layer, (2) loss of hairs on the gena and mandibular base and polished head, (3) cessation of all extranidal activities, (4) the most superior dominance, (5) receiving a great deal of food from the other workers, (6) remarkable prolongation of life span. Of these characteristic, (1) (2) and (3) are common to those of the queen of *Vespa* species in a populous colony, and agonistic behaviour involving dominance relationships is virtually absent between queen and workers, not only at food exchange but throughout their encounters. On the other hand, in colonies of the more socially primitive vespine wasps, such as *Mischocyttarus drewseni* and *Polistes* spp., the division of labour between queen and workers is principally

brought about by behavioural dominance (YOSHIKAWA 1963, MORIMOTO 1961, WEST-EBERHARD 1969, JEANNE 1972). A similar case is observed among foundresses of *Polistes* spp. in the primary pleometrotic colonies of *P. annularis* (RAU 1940), *P. gallicus* (PARDI 1943, DELEURANCE 1955) and *P. versicolor* (RICHARDS 1971). In these species the colonies are founded by a number of almost equipotential, mostly fertilized females, and the one with the most developed ovaries becomes the queen which forages much less than the subordinates or workers and receives a good deal of food from them; the others either become acting workers with ovarian regression or leave the nest as a result of competition.

In *Vespa* all workers in queen-right colonies seem to be almost entirely equipotential in reproductive functions compared with that of the queen. The conditions in the absence of a queen in the colony of *V. analis*, being of a small colony size, are very similar to those in a pleometrotic colony of some *Polistes* spp. as above mentioned. Therefore, it seems likely that the dominant worker of *V. analis* controls subordinates and prevents the development of ovaries in subordinates, which involves all the workers who emerged after the death of the queen.

However, very little aggressive or agonistical behaviour was seen after the establishment of the substitution queen, which became characterized by the polished head and the loss of body hairs like the queen of the species.

## V. POPULATION DYNAMICS

Hornets of the genus *Vespa* possess a complex mode of life, and their annual cycle is fundamentally divided into two basic phases, solitary and social, each of which occupies about half a year. Therefore, various theories of population ecology which have been applied to most conventional animal populations are not applicable to the case of *Vespa* species without appropriate modifications.

In this chapter, the population of *Vespa* species is treated at two levels, individual and colony. At the individual level the survivorship of colony members is mainly discussed in relation to the life tables obtained from workers in normally developed colonies. At the colony level I deal with some observations on the survival of nests, colony development and annual fluctuations of nests and some factors affecting them.

### 1. Survivorship curves of *Vespa* workers

#### 1) Length of developmental stage

Table 35 shows the variability of each stage and the total duration of brood development in workers of

Table 35. Length of each developmental stage in five *Vespa* workers (in days) and the size of adult workers.

Species	Egg	Larval instar					I-V	Cocoon	Total	No. of individ. observed	Size of adult workers* (mm)
		I	II	III	IV	V					
<i>V. simillima</i>	4.3 (0.2)	1.0 (0.0)	1.0 (0.0)	1.0 (0.2)	1.5 (0.4)	6.7 (1.2)	11.2 (1.2)	15.3 (0.4)	30.8 (2.5)	115	21.3
<i>V. crabro</i>	5.0 (0.2)	1.0 (0.0)	1.1 (0.1)	1.2 (0.2)	2.2 (0.5)	6.8 (2.1)	12.0 (2.5)	15.5 (0.3)	32.4 (4.7)	73	24.1
<i>V. analis</i>	5.0 (0.2)	1.0 (0.0)	1.0 (0.0)	1.3 (0.2)	2.1 (0.5)	6.5 (1.8)	11.9 (2.1)	15.6 (0.4)	32.4 (4.1)	60	24.5
<i>V. mandarina</i>	6.0 (0.1)	1.0 (0.0)	1.5 (0.0)	2.0 (0.1)	3.5 (0.6)	7.8 (1.9)	15.9 (2.2)	18.2 (0.4)	40.1 (4.6)	84	34.2
<i>V. tropica</i>	6.2 (0.1)	1.0 (0.0)	1.0 (0.0)	1.3 (0.1)	2.1 (0.6)	7.2 (2.2)	12.6 (2.5)	16.8 (0.5)	35.6 (4.7)	71	30.1

Parenthesized numbers show standard deviations ( $\pm$ ).

\* Mean of 10 workers for each species.



five *Vespa* species. Comparing the data, the lengths of the 5th instar larval stage vary widely, while the lengths of egg, immature larval stage, especially 1st-3rd instars, and cocoon stages are fairly constant in each species, though there seems to be some specific differences. Total duration of brood development from egg to adult varied on the average from 30.8 days in *V. simillima* in the smallest species in body size to 40.1 days in *V. mandarinia* in the largest species, and it is recognized that there is a tendency that the larger the body size in adult hornets, the longer the duration becomes among the five species.

## 2) Survivorship curves for all developmental stages

Figs. 59–63 present survivorship curves for all developmental stages of workers of five *Vespa* species, using the following parameters: (1)  $l_x$ , number of individuals alive at the beginning of each stage, (2)  $d_x$ , number of individuals failing during each stage, (3)  $q_x$ , number of individuals failing per 1000 alive at the beginning of each stage. Although all these data were prepared from well developed colonies at polyethic period, these five species show a general correlation between survivorship and mortality, and all the survivorship curves indicate basically similar features, i.e., remarkably low mortality during the immature

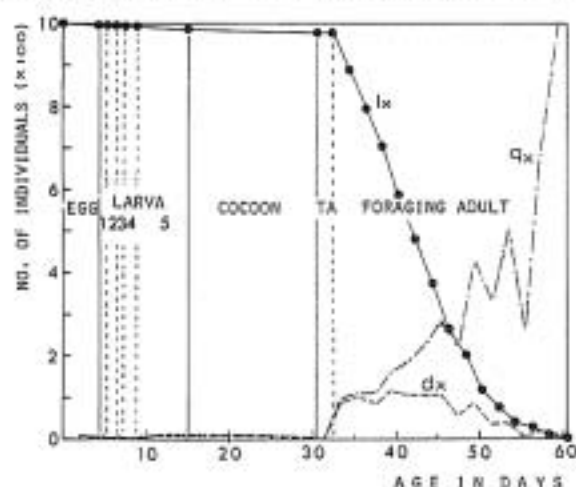


Fig. 59. Survivorship curve for *Vespa simillima* workers in a nest(S6801). TA: teneral adult. For  $l_x$ ,  $d_x$  and  $q_x$ , see text.

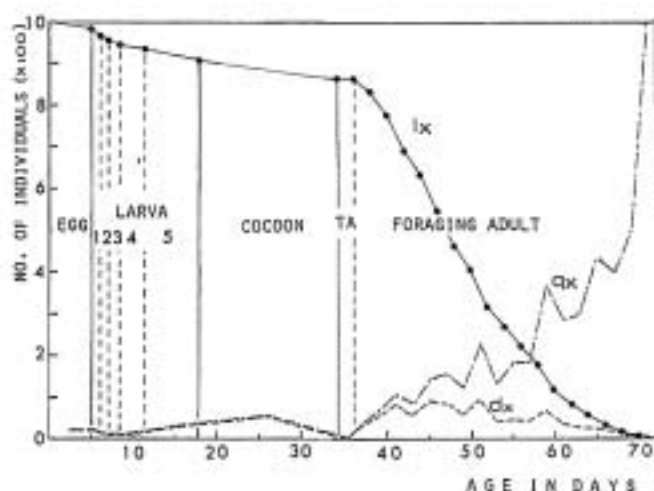


Fig. 60. Survivorship curve for *Vespa crabro* workers in a nest(C6601). TA: teneral adult. For  $l_x$ ,  $d_x$  and  $q_x$ , see text.



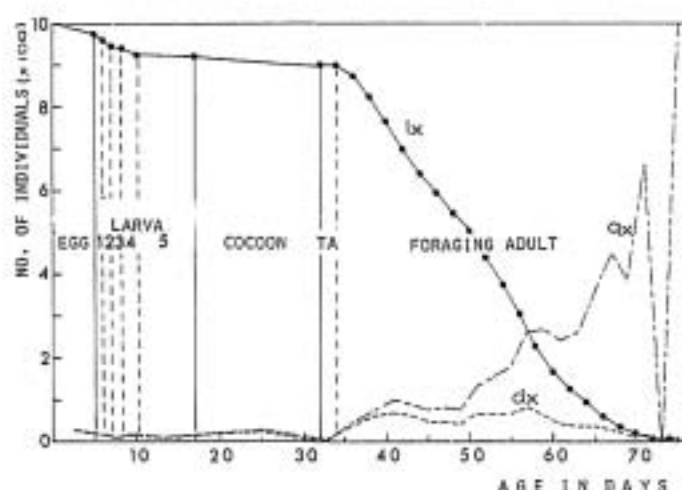


Fig. 61. Survivorship curve for *Vespa analis* workers in a nest(A7207). TA: teneral adult. For lx, dx and qx, see text.

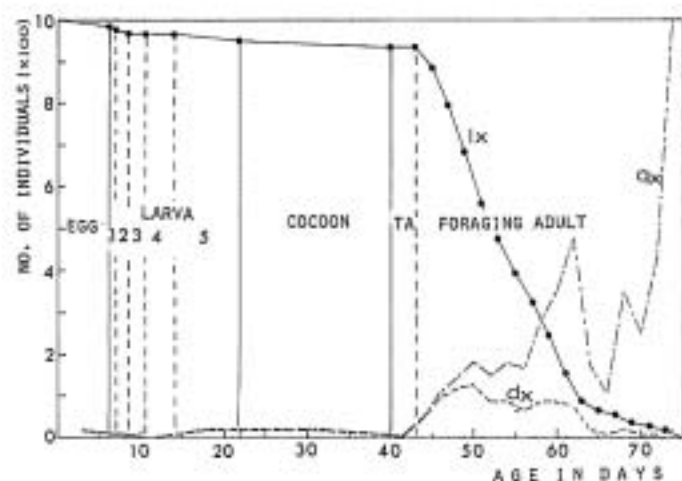


Fig. 62. Survivorship curve for *Vespa mandarinia* workers in a nest(M7401). TA: teneral adult. For lx, dx and qx, see text.

stages and high mortality after the commencement of foraging activities in the adult stage. Therefore, the survivorship curve is a convex type, and may be considered to be curve Type I in DEVEY's sense (DEVEY 1947).

### 3) Survivorship curves for adult workers

Fig. 64 shows survivorship and mortality curves for the same cohorts given in Figs. 59~63, but deals with adults alone at daily intervals. Survivorship curves for each species are closely similar and in general the maximum longevity is about twice as long as the mean longevity, though it is recognized that there are some differences among them. The mortality of *V. tropica* workers during the early adult stage is remarkably low as compared with that of the other four species. This difference seems to be due to the differences in their feeding habits and disposition as discussed later. A gradual decrease begins with the

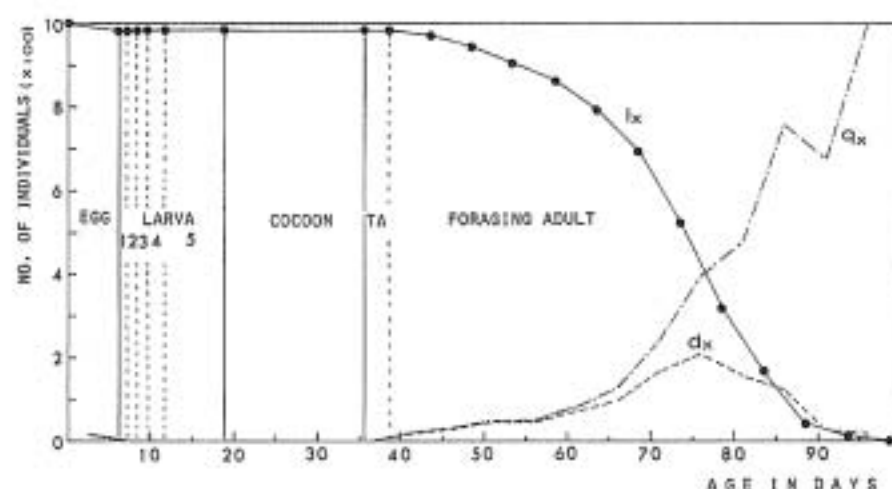


Fig. 63. Survivorship curve for *Vespa tropica* workers in a nest (T7401). TA: teneral adult. For  $l_x$ ,  $d_x$  and  $q_x$ , see text.

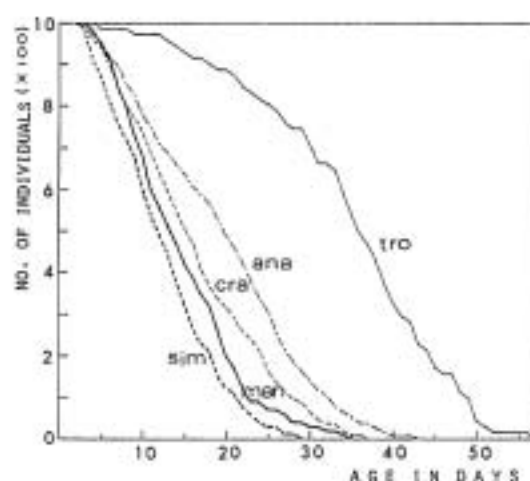


Fig. 64. Survivorship curves for adult workers of five *Vespa* species at daily intervals. *sim*: *V. similima*; *man*: *V. mandarinia*; *cra*: *V. crabro*; *ana*: *V. analis*; *tro*: *V. tropica*.

commencement of the first extranidal activity 2 or 3 days after their emergence in all curves except for *V. tropica*, and survival curves descend with a sigmoid shape in each species.

#### 4) Fate of brood at emergence of sexuals

The males and new queens are produced towards the end of the seasonal cycle. They feed on the secretion of the 5th instar larvae and the food brought in by the workers during the time they remain in the nest. However, it has been observed that many dead or weakened larvae are taken out of the cells and abandoned on the ground near the nest, with the appearance of the sexuals (DUNCAN 1939).

Table 36 shows the life tables for all members of the brood of a *V. tropica* colony (T7401), which is classified into three period according to the time when the eggs were laid; solitary period, co-operative periods before emergence of sexuals and after emergence of sexuals. These data indicate that brood development is clearly disturbed towards the later stages of the seasonal cycle. In the case of this nest, the

Table 36. Life table for *Vespa tropica* in one nest(T7401) at different nesting periods.

Period	Duration of oviposition (1970)	Developmental stage	Fdx**	lx**	dx**	qx**
Eggs laid before emergence of workers (n=39)*	June 9th - July 13th	Egg	—	39	0	0
		Larval instar	I	—	39	0
			II	—	39	0
			III	—	39	0
			IV	—	39	0
			V	—	39	0
		Cocoon	—	39	0	0
Eggs laid before emergence of sexuals (n=269)*	July 14th - Aug. 23rd	Adult	—	39	—	—
		Egg	Cannibalism by adults	269	7	2.6
		Larval instar	I	Cannibalism by adults	262	1
			II	—	261	0
			III	—	261	0
			IV	—	261	0
			V	Cannibalism by adults	261	77
Eggs laid after emergence of sexuals (n=98)	Aug. 24th - Sep. 25th	Cocoon	Cannibalism by adults	184	16	8.6
		Adult	—	168	—	—
		Egg	Cannibalism by adults	98	28	28.6
		Larval instar	I	Starvation	70	2
			II	Starvation	68	3
			III	Starvation	65	6
			IV	Starvation	59	7
			V	Starvation and unknown	52	47
		Cocoon	Cannibalism by adults	5	5	100.0
		Adult	—	0	—	—

\* No of eggs oviposited by the queen during each period.

\*\* See text.

mortality of brood was zero during the solitary period. High mortality occurred during the time of the 5th instar larvae and cocoons after mid-August.

It is clear from continuous observations that the mortality factors in the developmental stages during the later period were almost entirely due to cannibalism by workers and the sacrificed larvae and pupae were mostly those of males or new queens. This cannibalism is assumed to be caused by the lack of protein food which almost entirely depends on polistine brood, because the colonies of polistine wasps have already ceased their brood rearing after mid-August (Fig. 41).

During the period after emergence of sexuals higher mortality was observed throughout all developmental stages, particularly, egg and 5th instar larval stages, and no eggs were laid after the emergence of the

sexuals. In this period the mortality in the early developmental stages from egg to 3rd instar larva and cocoon stage was mainly due to cannibalism by workers. But it should be noted that the high mortality of the 5th instar larvae was mostly caused by starvation, not by cannibalism as was observed at the time before emergence of the sexuals.

Table 37 is a life table for brood of *V. analis* at the later stages of the seasonal cycle, and all the brood in the colony (A7207) were identified as either made or new queen. In this species a tendency similar to

Table 37. Life table for *Vespa analis* brood from eggs laid by the queen before and after emergence of the sexuals in one nest (T7207).

Period	Duration of oviposition (1972)	Developmental stage	Fdx**	lx**	dx**	qx**
Eggs laid before emergence of sexuals (n=124)	Aug. 12th ~ Sep. 24th	Egg	Cannibalism by adults	124	7	5.6
		Larval instar	I Cannibalism	117	2	1.7
			II —	115	0	0
			III Cannibalism	115	1	0.9
			IV Cannibalism	114	2	1.7
			V Cannibalism	112	35	31.2
		Cocoon	Cannibalism	77	14	18.0
Eggs laid after emergence of sexuals (n=82)	Sep. 25th ~ Nov. 10th	Adult (36 ♀♀ 27 ♂♂)		63	—	—
		Egg	Cannibalism	82	36	43.9
		Larval instar	I Cannibalism	46	2	4.3
			II Cannibalism	44	1	2.2
			III —	43	0	0
			IV Cannibalism	43	1	2.3
			V Starvation and unknown	42	39	92.8
		Cocoon	Cannibalism	3	3	100.0
		Adult		0	—	—

\* See text.

*V. tropica* is also recognized. About half of 124 eggs laid from August 12th to September 24th before emergence of the sexuals reached the adult stage and 36 new queens and 27 males emerged and departed from the nest. High mortality occurred particularly in the 5th larval and cocoon stages, and most of them died from cannibalism by workers. On the other hand, 43.9% of the eggs laid by the queen from September 25th to November 10th after emergence of the sexuals disappeared during the egg stage due to cannibalism by adult hornets, but 47.6% of them died from starvation towards the end of the colony cycle. Only three reached the cocoon stage but no adults emerged in this period.

Judging from these observations, together with other observations in many other nests, it is considered that the workers devote their attention mainly to nursing of adult sexuals which have emerged earlier; thus most of the larvae fail to be fed because of a decrease in attention given to them when the sexuals emerge. This behaviour of workers may be caused by the extreme claim for food supply by the adult sexuals.

## 2. Seasonal changes in the population structure of *Vespa* colonies

### 1) Number of cells

Fig. 65 shows the seasonal changes in the number of cells in the colonies of five *Vespa* species examined during 1966–1975.

*V. tropica*: The hibernated queens started to build their nests in early June, and most of the colonies lost their queen in September and nest activities ceased in about early October. Two queen nests collected in mid-June had 16 and 23 cells. The mean number of cells per colony was  $37.6 \pm \text{s.d. } 13.0$  ( $n=5$ ) in June, increasing to  $128.0 \pm \text{s.d. } 62.1$  ( $n=12$ ) in August and  $165.8 \pm \text{s.d. } 77.3$  ( $n=10$ ) in September, respectively.

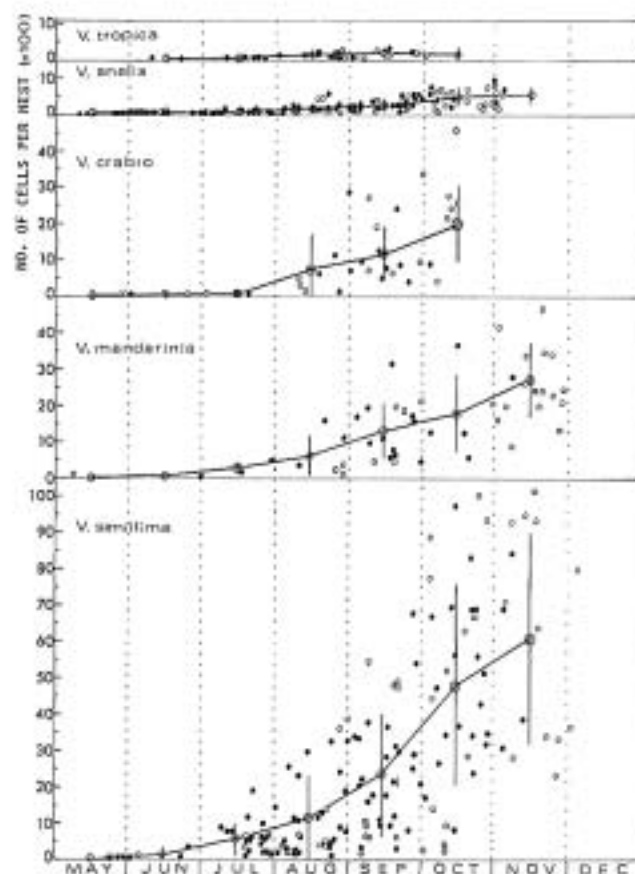


Fig. 65. Seasonal changes in the number of cells in the colonies of five *Vespa* species. Open circle, queenless colony; solid circle, queen-right colony; large open circle, monthly mean with standard deviation.

*V. analis*: The queens began their building activity in early to late May and the colonies lasted about six months until late October to early November, though 65.4% of surviving nests had lost their queen among 26 nests sampled in October. The mean number of cells per colony changed from  $69.1 \pm \text{s.d. } 54.8$  ( $n=15$ ) in July to  $516.7 \pm \text{s.d. } 190.1$  ( $n=7$ ) in early November. Queenless colonies increased noticeably after early August and 47.8% of all the nests which were collected from August to November had lost their queens.

*V. crabro*: The queens began their nesting activity in mid-May. Two queen nests collected in late May had 29 and 31 cells, respectively. The number of cells remained less than about 100 until mid-July, and then increased. The mean number of cells per colony changed from  $767.6 \pm \text{s.d. } 962.5$  ( $n=7$ ) in August to  $1,984.8 \pm \text{s.d. } 1,116.2$  ( $n=6$ ) in October.

*V. mandarina*: Queens probably began to establish their nests in early May to June, and the nesting activity ceased in late November. The queen nests contained 20 cells in early May and 40 cells in late June. The number of cells increased with the emergence of workers after July, and the mean number of

cells per colony changed from  $284.0 \pm \text{s.d. } 239.0$  ( $n=2$ ) in July to  $2,712.4 \pm \text{s.d. } 984.7$  ( $n=15$ ) in October. *V. similima*: Queen nests contained  $14.7$  cells  $\pm \text{s.d. } 2.1$  ( $n=3$ ) in late May. The number of cells increased greatly during early July, and increased again after July with the achievement of relocation of the nest site. Nesting activities were observed even in early December in some nests. The mean number of cells per colony changed from  $575.7 \pm \text{s.d. } 435.6$  ( $n=22$ ) in July to  $6,087 \pm \text{s.d. } 2,869.3$  ( $n=14$ ) in October.

The maximum number of cells per colony so far observed varied from 313 in *V. tropica* to 10,058 in *V. similima* (Table 38), and the number of cells produced is ranked as *similima*  $\gg$  *mandarinia*  $\approx$  *crabro*  $\gg$  *anis*  $>$  *tropica*.

Table 38. The number of cells in the largest nests of five *Vespa* species so far taken in and near Kibi.

Species	Nest code	Date	No. of cells	No. of combs
<i>V. tropica</i>	T7105	Sep. 18'71	313	3
<i>V. analis</i>	A7522	Oct. 29'75	752	4
<i>V. crabro</i>	C7307	Oct. 22'73	4,563	6
<i>V. mandarinia</i>	M6403	Nov. 21'64	4,661	6
<i>V. similima</i>	S6403	Nov. 23'64	10,058	11

## 2) Immature stages

The mean number of immatures in *Vespa* colonies are summarized in Figs. 66–70.

*V. tropica*: The number of eggs remained at 10–20 during June and July, reached a maximum of  $28.2 \pm \text{s.d. } 14.9$  ( $n=7$ ) in August, and egg production in most colonies ended by mid-September.

The number of larvae was also highest during August and the mean number of larvae was  $25.7 \pm \text{s.d. } 12.5$  ( $n=7$ ) for 1st–4th instars and  $21.3 \pm \text{s.d. } 18.1$  ( $n=7$ ) for 5th instar in this month. Fewer larvae of 1st–4th instars were found in most colonies in September, but the 5th instar larvae remained relatively constant during September.

Worker cocoons increased from 0 in June to  $15.6 \pm \text{s.d. } 14.2$  ( $n=7$ ) in August, and disappeared in September in most colonies. The mean number of cocoons of sexuals was  $18.7 \pm \text{s.d. } 23.7$  ( $n=10$ ) for queens and  $6.7 \pm \text{s.d. } 11.5$  ( $n=7$ ) for males in August, and was  $7.4 \pm \text{s.d. } 16.7$  ( $n=11$ ) for queens and  $4.5 \pm \text{s.d. } 7.3$  ( $n=10$ ) for males in September.

*V. crabro*: The mean number of eggs per colony remained less than 32 until July, and then reached a maximum of  $152.0 \pm \text{s.d. } 138.2$  ( $n=13$ ) in September. Rapid decline occurred in early October and few eggs were found in most colonies in mid-October.

The number of larvae was also highest in September and the mean was  $174.6 \pm \text{s.d. } 167.1$  ( $n=13$ ) for 1st–4th instars and  $239.1 \pm \text{s.d. } 209.7$  ( $n=13$ ) for 5th instar in September. Numbers of larvae of all instars decreased rapidly after mid-October. The maximum number of larvae per colony in September was 668 for 1st–4th instars and 719 for 5th instar in a nest (C7504) collected on September 9th, 1975.

Cocoons were found in low numbers (2–27) until July. The mean number of worker cocoons was  $123.7 \pm \text{s.d. } 106.3$  ( $n=7$ ) in August with a maximum of 335 in a nest (C7304), and declined during September. Colonies contained no worker cocoons in October. Cocoons of sexuals first appeared in late August in a few colonies, and the peak populations, which were found with mean number of  $85.2 \pm \text{s.d. } 133.2$  ( $n=10$ ) for new queen and  $185.9 \pm \text{s.d. } 275.5$  for male in September, declined rapidly toward October. The maximum number of cocoons of sexuals per colony was 420 for new queen (C7507) and 885 for male (C7504).

*V. mandarinia*: The mean number of eggs per colony increased from 38 (M7401) in July to  $176.8 \pm \text{s.d. } 120.7$  ( $n=16$ ) in September and thereafter declined during October and disappeared in late November. During August numbers of larvae were probably highest in each stage. Immatures of 1st–4th instars decreased thereafter and disappeared by late November. The mean number of 5th instar larvae in September remained  $234.3 \pm \text{s.d. } 162.4$  ( $n=6$ ) in August and decreased gradually during November. The maximum



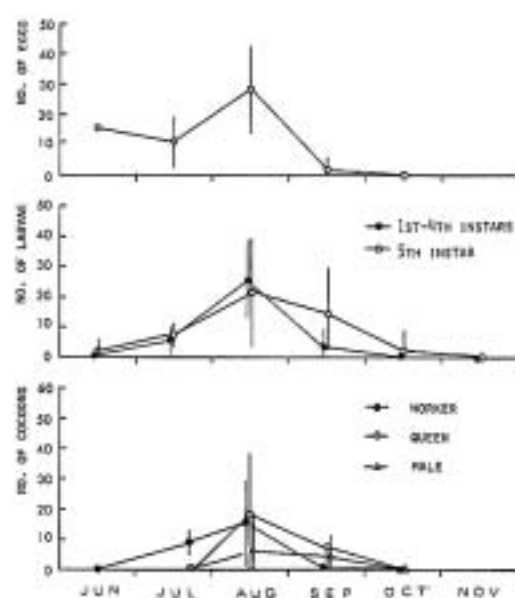


Fig. 66. Seasonal change in monthly mean number of immature stages in colonies of *Vespa tropica*. Vertical line shows standard deviation.

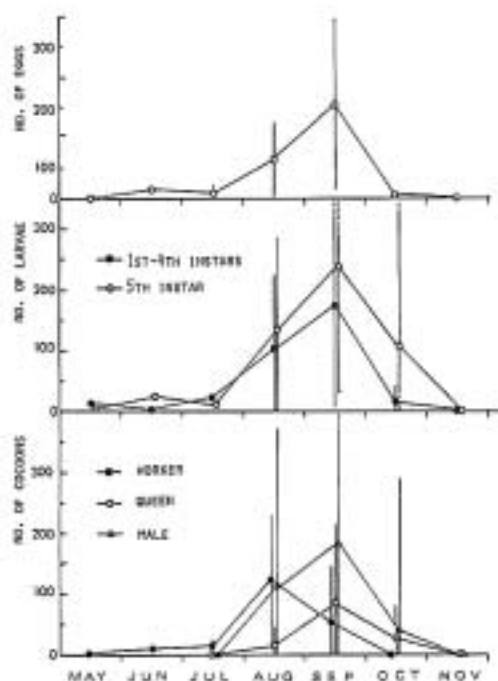


Fig. 67. Seasonal change in monthly mean number of immature stages in colonies of *Vespa crabro*. Vertical line shows standard deviation.

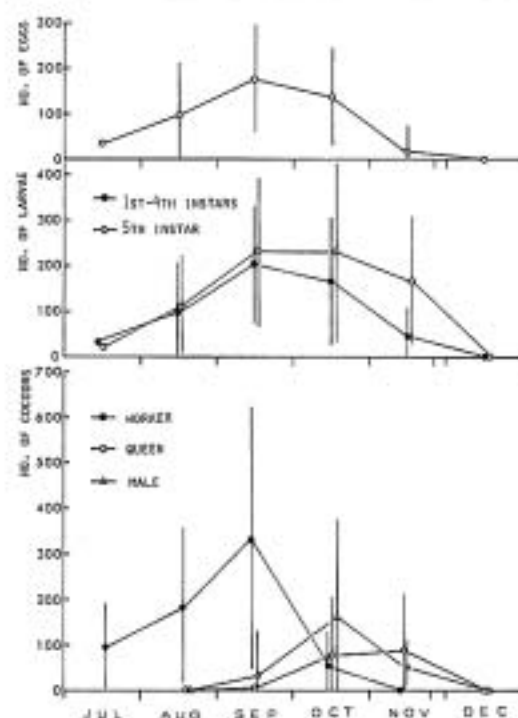


Fig. 68. Seasonal change in monthly mean number of immature stages in colonies of *Vespa mandarinia*. Vertical line shows standard deviation.

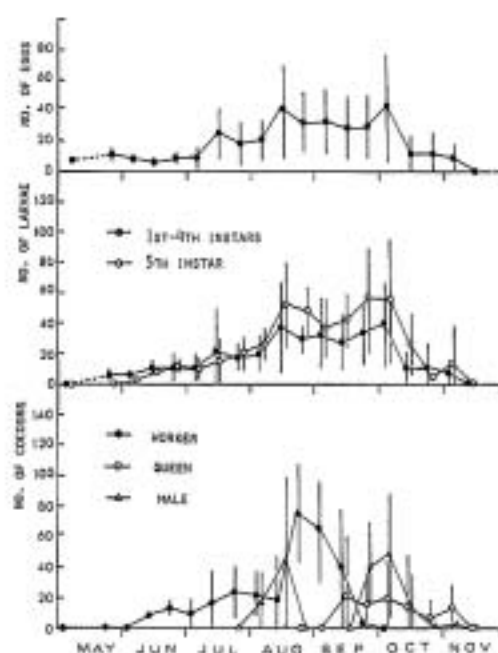


Fig. 69. Seasonal change in monthly mean number of immature stages in colonies of *Vespa analis*. Vertical line shows standard deviation.

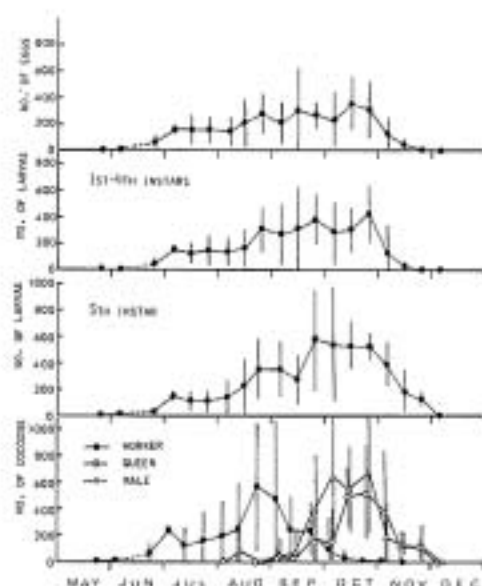


Fig. 70. Seasonal change in monthly mean number of immature stages in colonies of *Vespa similima*. Vertical line shows standard deviation.

number of larvae per colony was 452(M7201) for 1st–4th instars and 637(M7202) for 5th instar in September in a nest(M7201) collected on September 19th, 1972.

The number of worker cocoons changed from  $95.0 \pm \text{s.d. } 96.2$  in July to  $337.2 \pm \text{s.d. } 286.7$  ( $n=16$ ) in September and thereafter declined rapidly, disappearing in November in most colonies. Cocoons of sexuals first appeared in late August in a few colonies. The number of male cocoons reached a peak in October and that of new queen was  $88.3 \pm \text{s.d. } 130.1$  ( $n=16$ ) in November; both disappeared in December. The maximum number of worker, male and new queen cocoons per colony was 1,015(M7201) in mid-September, 532(M6902) in mid-October and 491(M7503) in early November, respectively.

*V. analis*: The mean number of eggs per colony did not exceed ca. 10 until early July and thereafter increased from  $18.0 \pm \text{s.d. } 15.0$  ( $n=6$ ) in late July to  $42.2 \pm \text{s.d. } 36.8$  ( $n=9$ ) in early October, with a maximum of 99 in a nest(A6706) collected on August 17th, 1967. The number of eggs declined rapidly during mid-October and early November.

The number of immature larval stages of 1st–4th instars changed approximately equally to that of eggs throughout the nesting period, and the maximum number of immature larval stages per colony was 89 in a nest (A6821) collected in early October. The mean number of 5th instar larvae remained less than that of immature stages until mid-June, but increased from less than 20 per colony during July to a peak of  $56.8 \pm \text{s.d. } 36.8$  ( $n=12$ ) in late September. Few larvae were found in colonies in mid-November.

The cocoons of workers first appeared in early to mid-June. The mean number of cocoons of workers increased greatly with a maximum of  $75.4 \pm \text{s.d. } 32.3$  ( $n=5$ ) per colony in late August and thereafter declined rapidly by late September. Male cocoons first appeared in some colonies during early to mid-August and were not found in any of the colonies collected during the period from late August to early September and reappeared after late September in every colony. New queen cocoons were first observed in mid-September. Cocoons of both sexuals were found until early November. The mean number of male cocoons reached a peak of  $49.9 \pm \text{s.d. } 44.1$  ( $n=7$ ) in early October and that of new queen cocoons fluctuated from  $2.6 \pm \text{s.d. } 2.8$  ( $n=7$ ) in early November to  $20.9 \pm \text{s.d. } 26.8$  ( $n=7$ ) in early October. The maximum number of male and new queen cocoons present per colony was 127 (A7519) and 80 (A6821) in early October, respectively.

*V. similima*: The mean number of eggs pr colony changed from  $7.3 \pm \text{s.d. } 3.8$  ( $n=3$ ) in late May to  $354.2 \pm \text{s.d. } 208.5$  ( $n=9$ ) in mid-October, and thereafter declined during November, then disappeared in early December. The maximum number of eggs present per colony was 1,255 in a nest (S7010) collected on September 17th, 1970.

The mean number of immature larvae fluctuated approximately equally to that of eggs throughout nesting period. The maximum number of immature larval stages per colony was 1,218 in the nest mentioned above.

The mean number of 5th instar larvae was also approximately equal to those of immature larval stages until early August, and thereafter fluctuated from  $221.3 \pm \text{s.d. } 208.9$  ( $n=8$ ) in mid-August to  $127.0 \pm \text{s.d. } 18.4$  ( $n=3$ ) in late November with a maximum of  $588.4 \pm \text{s.d. } 392.3$  ( $n=10$ ) in late September. The maximum number of 5th instar larvae present per colony was 1,336 in a nest (S6902) collected on October 4th, 1969.

Cocoons first appeared in early June. The mean number of worker cocoons increased rapidly compared with that of the other *Vespa* species, and reached a maximum of  $563.4 \pm \text{s.d. } 496.7$  ( $n=10$ ) in late August and thereafter decreased to  $2.2 \pm \text{s.d. } 4.3$  ( $n=12$ ) in late October, then disappeared by mid-November. Male cocoons first appeared in mid-August in a few colonies, but were not found in any colonies collected in late August. During the period from early to mid-September 8 out of 24 colonies contained male cocoons and the percentage of the colonies with male cocoons reached 80% (8/10) in late September. The mean number of male cocoons was  $628.0 \pm \text{s.d. } 532.1$  ( $n=11$ ) in early October and increased to  $668.0 \pm \text{s.d. } 449.4$  ( $n=12$ ) in late October, and thereafter decreased rapidly during November. The maximum number of male cocoons per colony was 1,743 in a queenless nest (S7021) collected on October 21st, 1970. New queen cocoons were found during the period from late August to November. The mean number of cocoons pr colony remained less than 20 until mid-September and thereafter increased rapidly to  $511.6 \pm \text{s.d. } 342.0$  ( $n=12$ ) in late October and then declined during November. The maximum number of new queen cocoons per colony was 1,380 in a nest (S6606) collected on October 27th, 1966.

### 3) Adult hornets:

*V. tropica*: Workers began to emerge in late July and a few of them were still present in mid-October (Fig. 71). The mean number of workers per colony was  $0.4 \pm \text{s.d. } 0.9$  ( $n=5$ ) in July and increased to  $12.6 \pm \text{s.d. } 9.2$  ( $n=12$ ) in August, and thereafter declined during September. The maximum number of

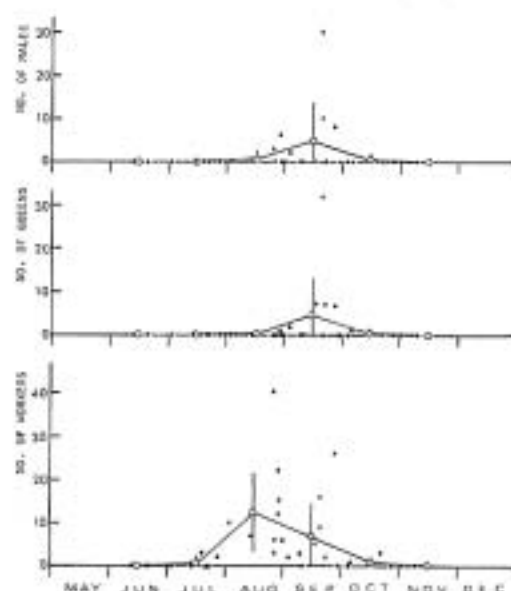


Fig. 71. Seasonal changes in number of adults in colonies of *Vespa tropica*. Open circle and vertical line indicate monthly mean and standard deviation.

workers present per colony was 40 in a nest (T7303) collected on August 23rd, 1973. Males began to emerge in late August. In September the mean number of males per colony was  $4.9 \pm \text{s.d. } 8.9$  ( $n=13$ ) with a maximum of 30 per colony (T7104). New queens also began to emerge in late August. The mean number of new queens was approximately equal to that males throughout the emergence period. The maximum number of new queen per colony was 32 in a nest (T7105) collected on September 19th, 1971.

*V. crabro*: Workers began to emerge from mid- to late June (Fig. 72). The mean number of workers increased from  $10.3 \pm \text{s.d. } 6.7$  ( $n=3$ ) in July to  $162.4 \pm \text{s.d. } 74.2$  ( $n=12$ ) in September with a maximum of 426 in a colony (C6802) collected on August 30th, 1968. It decreased rapidly to  $52.2 \pm \text{s.d. } 58.3$  ( $n=11$ ) in October and workers disappeared in most colonies in early November. The first males appeared from mid- to late August in a few colonies. The mean number of males changed from  $1.7 \pm \text{s.d. } 4.1$  ( $n=7$ ) in August to  $51.5 \pm \text{s.d. } 130.1$  ( $n=11$ ) in October. The maximum number of males was 434 in a queenless nest (C7508) collected on October 1st, 1975. New queens first appeared in a few colonies from mid- to late September. The mean number of new queens was  $38.9 \pm \text{s.d. } 71.2$  ( $n=11$ ) in October with a maximum of 217 in a nest (C7405) collected on October 13th, 1974. In November new queens were not found in any colonies.

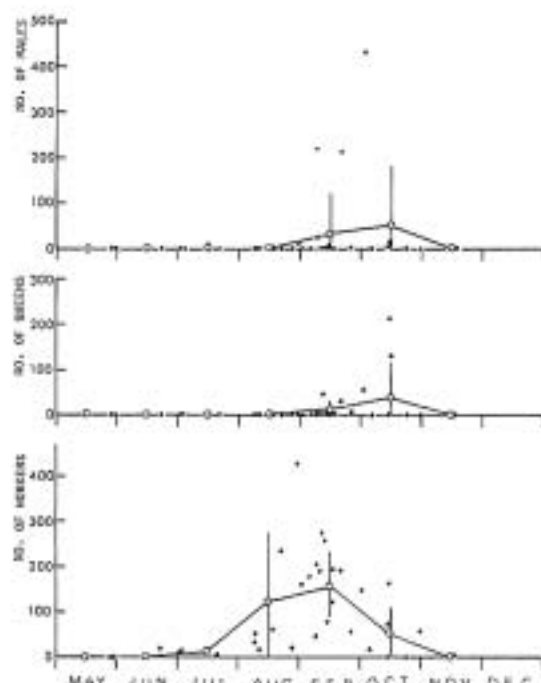


Fig. 72. Seasonal changes in number of adults in colonies of *Vespa crabro*. Open circle and vertical line indicate monthly mean and standard deviation.

*V. mandarinia*: Workers began to emerge from mid- to late June (Fig. 73). The mean number of workers increased from  $47.0 \pm \text{s.d. } 46.7$  ( $n=2$ ) in July to  $178.6 \pm \text{s.d. } 140.2$  ( $n=4$ ) in September with a maximum of 514 in a nest (M7202) collected on September 19th, 1972. Thereafter the numbers decreased to  $91.1 \pm \text{s.d. } 60.2$  ( $n=16$ ) in November.

Males first appeared in a few colonies from late August to September. The mean number of males increased from  $11.9 \pm \text{s.d. } 30.2$  ( $n=14$ ) in September to  $74.1 \pm \text{s.d. } 97.0$  ( $n=16$ ) in November when all the active colonies contained males. The maximum number of males present per colony was 284 in a nest (M6708) collected on November 25th, 1967.

New queens were not found in any colonies until November except for one nest with only 8 queens

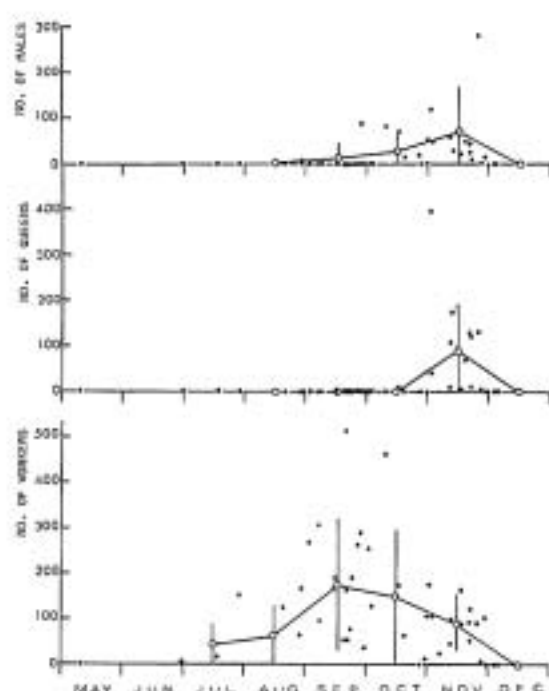


Fig. 73. Seasonal changes in number of adults in colonies of *Vespa mandarinia*. Open circle and vertical line indicate monthly mean and standard deviation.

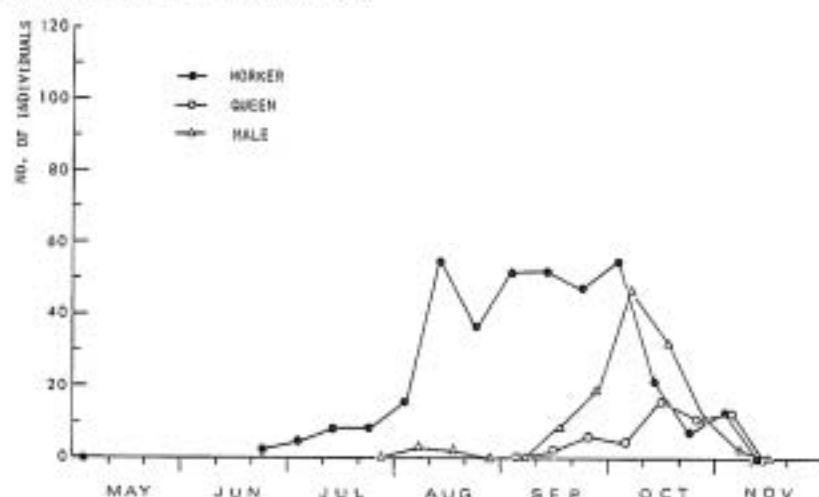


Fig. 74. Seasonal changes in number of adults in colonies of *Vespa analis* (10-day means).

(M7402) collected on October 17th, 1974. The mean number of new queens per colony was  $74.1 \pm \text{s.d. } 97.0$  ( $n=16$ ) in November with a maximum of 396 in a nest (M7403) collected on November 2nd, 1974. Adult hornets were not found in colonies excavated in December.

*V. analis*: Workers began to emerge from late June to early July (Fig. 74). Their numbers did not exceed 20 per colony until late July and thereafter increased rapidly during the time from mid-August to early September. The mean number of workers per colony fluctuated between  $36.7 \pm \text{s.d. } 24.7$  ( $n=5$ ) in late



August and  $54.9 \pm \text{s.d. } 52.5$  ( $n=9$ ) in mid-August. Numbers of workers declined sharply after mid-October, and workers disappeared in mid-November. The maximum number of workers was 142 in a nest (A7513) collected on August 20th, 1975.

Males were first found in a few queenless colonies collected from early to mid-August, and thereafter disappeared until mid-September. When males reappeared, the mean number per colony changed from  $8.4 \pm \text{s.d. } 18.2$  ( $n=5$ ) in mid-September to  $46.8 \pm \text{s.d. } 28.3$  ( $n=9$ ) in early October with a maximum of 84 males in a nest (A7519) collected on October 7th, 1975. Their numbers then decreased sharply to  $2.1 \pm \text{s.d. } 3.8$  ( $n=8$ ) in early November.

New queens began to emerge from mid- to late September. The mean number of the new queens per colony fluctuated from mid-October to early November between  $10.8 \pm \text{s.d. } 19.2$  ( $n=9$ ) in late October and  $12.1 \pm \text{s.d. } 23.3$  ( $n=8$ ) in early November with a maximum of 77 in a nest (A7111) collected on October 19th, 1971. Adult hornets were absent from colonies by mid-November.

*V. similima*: The first workers began to appear from mid- to late June and thereafter the number of workers increased rapidly (Fig. 75), compared to that of the other species. The mean number of workers

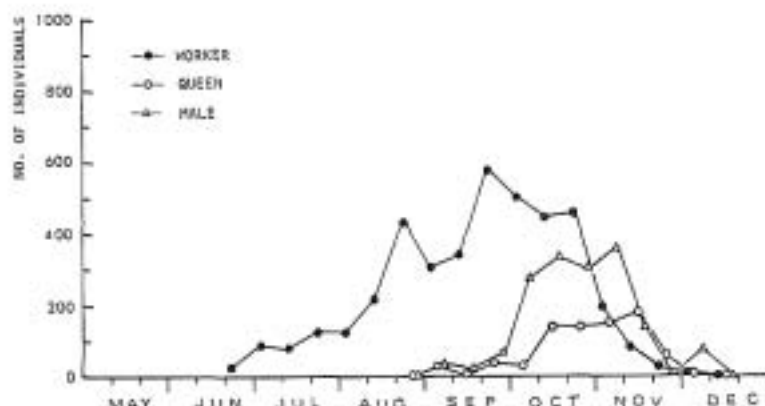


Fig. 75. Seasonal changes in number of adults in colonies of *Vespa similima* (10-day means).

per colony increased to over 120 by late July and attained a maximum number of  $574.9 \pm \text{s.d. } 395.8$  ( $n=11$ ) per colony in late September (Fig. 75). During October their numbers fluctuated between  $442.6 \pm \text{s.d. } 356.5$  and  $501.7 \pm \text{s.d. } 489.7$ , and declined sharply during November. The proportion of colonies with workers over 400 was 54.5% (6/11) in colonies collected in late October, but it decreased to 25.0% (2/8) in early November. Workers were still found in some colonies from late November to early December and disappeared at mid-December. The maximum number of workers present colony was 1,384 in a nest (S6603) collected on October 5th, 1966.

Males were first observed in two queenless colonies in early September and thereafter appeared both in queenright and queenless colonies. The mean number of males per colony increased from  $31.5 \pm \text{s.d. } 77.1$  ( $n=13$ ) in early September to  $357.4 \pm \text{s.d. } 301.6$  ( $n=8$ ) in early November, fluctuating at levels of over 300 per colony from mid-October to early November, and thereafter declined rapidly to  $6.4 \pm \text{s.d. } 9.0$  ( $n=5$ ) in late November, though many more were found in a few colonies collected in early December. The maximum number of males present per colony was 1,814 in a queenless colony (S7315) collected on October 5th, 1973, which had never produced any new queens, and 661 in a queenright colony (S6605) collected on October 27th, 1966.

New queens began to emerge in a few colonies from early to mid-September, and thereafter gradually increased until mid-November. The mean number of new queens per colony changed from  $31.5 \pm \text{s.d. } 77.1$  ( $n=13$ ) in early September to  $180.6 \pm \text{s.d. } 112.5$  ( $n=5$ ) in mid-November, fluctuating at about 135 during mid-October to mid-November. Thereafter the numbers declined rapidly to  $2.3 \pm \text{s.d. } 4.0$  ( $n=3$ )

in early December. The maximum number of new queens present per colony was 350 in a nest (S6811) collected on November 3rd, 1968.

### 3. Seasonal development of a single colony of *Vespa tropica*

It is very difficult to follow the development of individual colonies of *Vespa* during their active period from nest foundation to disintegration, because views of the inner nest are interrupted by a thick envelope, especially at the later stage of nesting. However, in *V. tropica* the envelope is incomplete and the lowest comb is always exposed within the nest cavity. This facilitates direct observation of populations inside a colony without disturbing it too much. Changes in the colony development and population structure of a single nest (T7401) of *V. tropica* are shown in Figs. 76 and 77 throughout the active season.

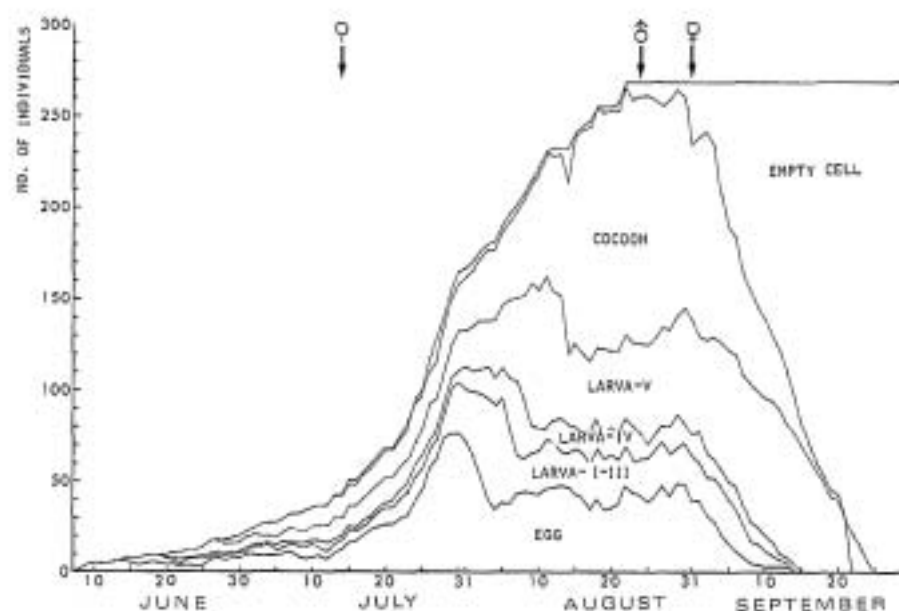


Fig. 76. Seasonal change of brood populations in a *Vespa tropica* colony (T7401). Arrows denote the day of the first emergence of each caste.

#### 1) Cell construction

In this colony the queen began to found her nest on June 9th, 1974 and built 42 cells alone until the time when the first workers emerged on July 14th. In the period from nest initiation to worker emergence the mean number of cells constructed per day was  $1.1 \pm \text{s.d. } 1.3$  (range: 0–6). After worker emergence the number of cells increased rapidly and a second comb was built on July 20th and a third one on August 7th, all these mainly constructed by workers. The nest reached its maximum on August 21st; at the time the nest was composed of 268 cells within 3 combs. The mean number of cells constructed per day was  $4.9 \pm \text{s.d. } 3.4$  (range: 0–15) during the period from worker emergence to final cell construction. The number of empty cells was very few throughout the solitary period and rarely exceeded 6.0% of the total number of cells until the emergence of sexuals, because empty cells either newly constructed or after emergence were generally supplied with an egg as soon as they were vacant. Thereafter, the empty cells increased rapidly due to the cessation of oviposition and cannibalism of brood stages.

#### 2) Immature stages

As the queen laid eggs only in newly constructed cells during the solitary period, the rate of oviposition was very similar to that of cell construction. She laid an average of  $1.4 \text{ eggs} \pm \text{s.d. } 1.8$  (range: 0–4) per day for the first 35 days from nest initiation to the first appearance of workers. After worker emergence

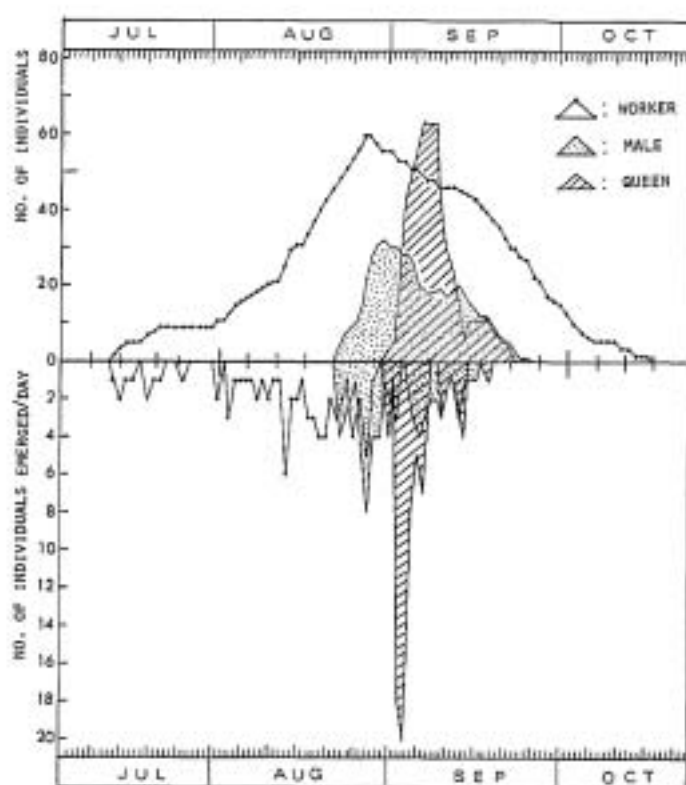


Fig. 77. Daily change of adult populations in a *Vespa tropica* colony (T7401).

the oviposition rate increased rapidly and the highest rate reached 14 eggs per day on July 27th and 28th. The highest total number of eggs was 76, observed 15 and 16 days after worker emergence. Thereafter, the total number of eggs decreased without recovery, though it varied between 34 and 48 during August and declined rapidly in early September. The queen stopped ovipositing on September 13th and died on September 20th, and all eggs disappeared on September 14th.

In the larval stages, 1st to 4th instar larvae reached their peak in total number in early August with a maximum of 73 larvae on August 5th, and it resulted in a rise in number of 5th instar larvae after about one week when they occupied nearly 75% of all the larvae present.

The number of cocoons reached a peak in late August when they occupied nearly 52.5% of all the brood with a maximum of 137 cocoons per day on August 25th.

All the brood stages decreased rapidly with the commencement of the emergence of sexuals. Eggs and immature larvae of 1st to 3rd instars first disappeared on September 14th, and 4th instar on the following day. Cocoons disappeared on September 21st, but the 5th instar larvae remained until September 24th.

### 3) Adult hornets

The first worker emerged 36 days after colony foundation. The increase in the number of workers was very slow during the early nesting period, and the total number of workers was less than 10 for the first 18 days after first emergence. Emergence of workers lasted for 44 days and stopped on August 28th. The number of workers reached a maximum of 60 on August 26th and 27th, just before emergence of sexuals, and thereafter declined. Activity worker was observed as late as October 14th. The total number of workers produced in this colony was 71, and the rate of emergence was  $1.7 \pm \text{s.d. } 1.2$  ( $n=44$ ) workers per day with a maximum of 6 workers per day.

The first males emerged 67 days, and the first new queens emerged 74 days after colony foundation. All males emerged in 25 days and all new queens in 18 days; the last emergence of both sexuals was on September 19th. The total number of sexuals produced in this colony was 61 males and 75 new queens. An explosive emergence occurred in the first half of the emergence period with an increase to 18 and 20 queens per day on September 1st and 2nd. Both sexuals stayed for about two weeks in the nest: males began to depart on and after September 1st, new queens from September 10th. All had left the nest by late September.

#### 4. Production of sexuals

##### 1) Number of sexuals produced per colony

The new queens and males are produced in the later part of colony development when the number of workers reaches a peak. Table 39 shows the specific difference in total number of sexuals in autumn nests of five *Vespa* species, based upon both adult hornets present in the nest and cocoons of each sex, which

Table 39. The number of sexuals produced per colony in five *Vespa* species.

Species	No. of new queens present			No. of males present			$\frac{Q}{R+B}$ (C/C+E)	No. of workers present	No. of cells (G)	Correlation coefficient between C and G	Nest code
	Cocoon (A)	Adult (B)	A + B (C)	Cocoon (D)	Adult (E)	D + E (F)					
<i>V. tropica</i> n=6*	$\bar{x}$ 28.6 (23.6)	8.2 (12.1)	36.8 (26.8)	11.0 (11.0)	4.8 (3.8)	15.8 (10.8)	0.65 (0.30)	18.5 (14.1)	207.0 (71.1)	r=0.348	
	min. 0	2	2	15	2	17	0.11	2	126		T7304
	max. 56	0	56	34	3	27	0.88	40	275		T7303
<i>V. analis</i> n=20*	$\bar{x}$ 27.7 (22.8)	13.0 (21.4)	40.7 (36.8)	31.3 (36.4)	32.7 (26.6)	64.0 (34.6)	0.45 (0.32)	53.4 (32.1)	498.3 (179.9)	r=0.472	
	min. 4	8	12	1	4	5	0.71	21	225		A7313
	max. 74	77	151	0	6	6	0.96	34	707		A7311
<i>V. crabro</i> n=13*	$\bar{x}$ 79.5 (119.8)	27.8 (39.3)	107.4 (122.5)	131.0 (207.8)	58.2 (128.7)	189.2 (316.4)	0.54 (0.33)	140.8 (76.4)	1,378.3 (958.5)	r=0.352	
	min. 28	4	32	4	1	5	0.39	53	327		C7302
	max. 420	35	455	188	212	400	0.53	192	2,476		C7307
<i>V. mandarinia</i> n=12*	$\bar{x}$ 101.0 (105.1)	107.7 (107.8)	208.7 (159.5)	117.9 (147.5)	94.3 (99.1)	212.2 (176.8)	0.50 (0.21)	136.2 (111.8)	2,346.7 (1,021.7)	r=0.584 (p<0.1)	
	min. 0	8	8	14	20	34	0.19	22	822		M7107
	max. 333	0	333	532	85	617	0.35	458	3,680		M6902
<i>V. simillima</i> n=21*	$\bar{x}$ 558.0 (371.8)	137.2 (111.3)	696.0 (467.8)	567.0 (535.6)	289.6 (208.3)	856.6 (460.6)	0.42 (0.31)	510.2 (315.4)	5,465.9 (2,336.9)	r=0.856 (p<0.001)	
	min. 16	0	36	170	3	173	0.09	81	949		S7317
	max. 1,380	320	1,692	462	661	1,123	0.60	471	9,323		S6605

Figures in parentheses denote s.d.(=). \* No. of nests observed.

could be easily distinguished from one another by the thickness and length of cell capping as reported by SPRADBERY (1971) and MacDONALD et al.(1974) for *Vespa* species. The maximum number of sexuals present varied from 56 new queens and 27 males in a *V. tropica* nest (T7303) to 1,692 new queens and 1,123 males in a *V. simillima* nest (S6605) and the number of sexuals produced per colony is ranked as *simillima* > *mandarinia* > *crabro* > *analis* > *tropica*.

It seems likely that the production of sexuals, especially new queens, depends greatly upon the colony size not only among different species but also among conspecific colonies, though correlation between number of cells and that of new queens produced in the same species is not clear except for *V. simillima* (Table 39). In the case of *V. simillima* there seems to be a strong correlation between the number of new queens produced with that of cells constructed, especially in the nests taken in October (Fig. 78). The

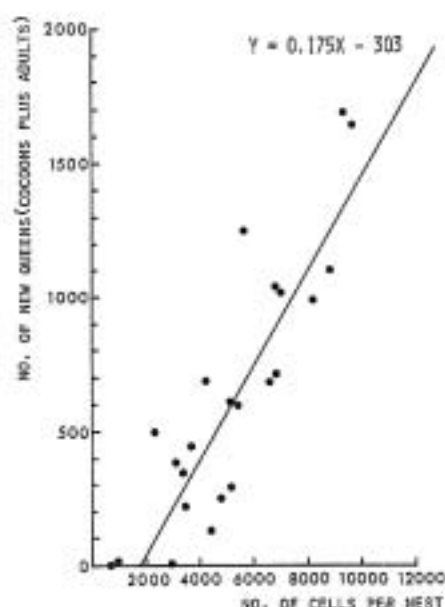


Fig. 78. Correlation of number of cells with number of new queens present per colony of *Vespa simillima* taken during October.

large successful colonies exceeding ca. 8,000 cells had usually more than 1,000 new queens present as well as males, while a poor colony such as S7317 with 949 cells in October had only 16 queens, though some may have been produced in the course of colony development.

This may suggest that the number of cells in a reproductively successful colony of *V. simillima* needs to reach a colony level of at least 1,000 cells, and only colonies attaining sufficient size have the ability to produce new queens.

Comparing this minimum size with the other species, the number of cells produced before and during the new queen rearing period is estimated on the basis of Table 39 (though data on each species are not sufficient in number) as follow: *V. mandarinia*, ca. 800 cells; *V. crabro*, ca. 300 cells; *V. analis*, 200 cells and *V. tropica*, ca. 100 cells.

On the other hand, some of the nests which have lost their initial queen before beginning queen production reach or often exceed such a number of cells, but produce only male hornets.

## 2) Larva:worker ratio

In addition to the adequate colony size in the number of cells in each species, it is recognized that there exist several other factors which promote new queen production. The change in the larva:worker ratio is one of the most important factors which favours the production of new queens as reported in bumble bees (RICHARDS and RICHARDS 1946, CUMBER 1949) and in other social wasps (RICHARDS and RICHARDS 1951, SPRADBURY 1979, ARCHER 1972).

Fig. 79 shows the seasonal change of larva:worker ratio in colonies of five *Vespa* species. The ratio remained generally high during the period prior to the production of new queens in all species. The ratios became much lower before the period when colonies began to produce queen brood, and during the period when colonies had reared queen brood to the cocoon stage, the ratio approached less than 2.0. Then the ratio became irregular as the new queens and males began to emerge in the nest.

On the other hand, it would appear that the change in larva:worker ratio is concerned basically with the number of workers present in each species. Fig. 80 shows that the larva:worker ratio is related to the number of workers present in colonies of *V. simillima* and *V. analis* before the period of the emergence

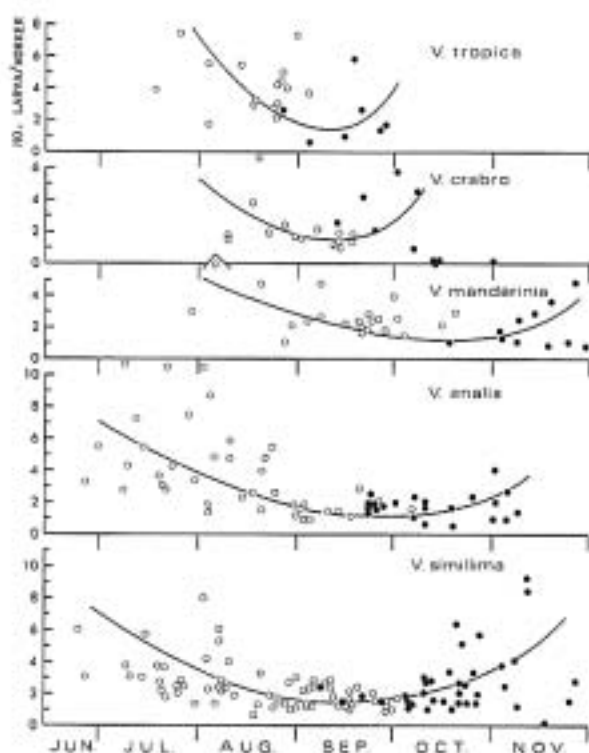


Fig. 79. Seasonal changes of larva/worker ratio in colonies of five *Vespa* species. Open circles: colonies with only worker brood; solid circles: colonies with new queens present.

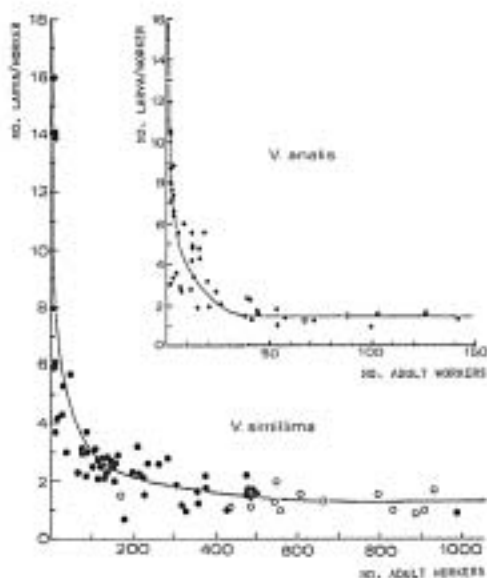


Fig. 80. Comparison of larva/worker ratios in relation to the numbers of workers present in colonies of *V. similis* (lower) and *V. analis* (upper) before the period of the emergence of new queens. Open circles: new queen cocoons present; solid circles: worker brood only.



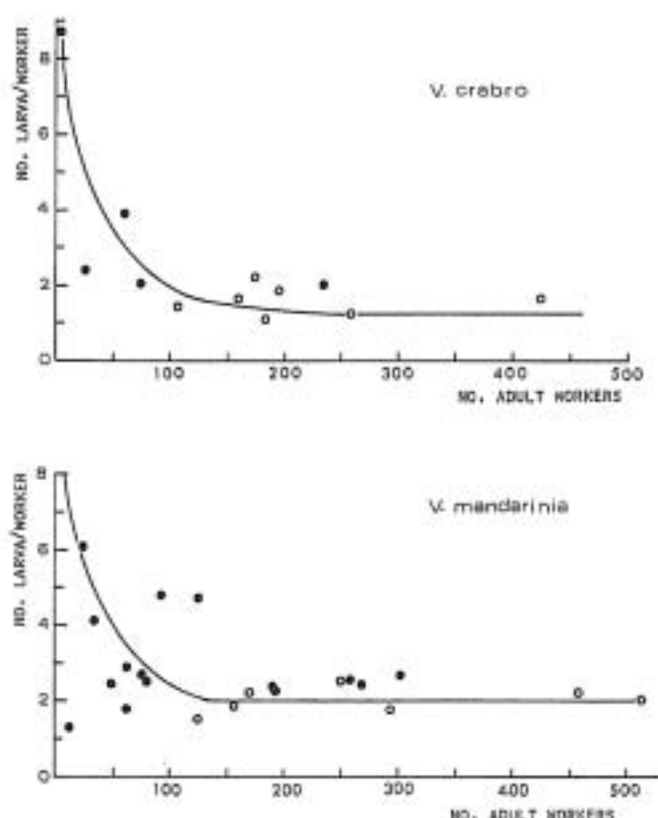


Fig. 81. Larva/worker ratios of the two *Vespa* species, *V. crabro* (upper) and *V. mandarinia* (lower). Open circles: new queen cocoons present; solid circles: worker brood only.

of new queens. Despite the remarkable difference in colony size between the two species there exists a conspicuous similarity in larva:worker ratios; the ratios in both species are approximately equal and the values for the queen rearing period varied only between 2.0 and 1.0. In *V. similima* such values in the ratios of larva:worker were likely to be constant among colonies with more than about 300 workers, and the values in the colonies with 50~300 workers varied almost entirely between 3.0 and 2.0, and those in the colonies with less than 50 workers were very much higher. On the other hand, in the case of *V. analis* the ratio fell below 2.0 when the colony had more than ca. 40 workers, and it increased rapidly in the colonies with less than ca. 20 workers.

Fig. 81 shows the larva : worker ratios of colonies of *V. crabro* and *V. mandarinia*, which are very similar in colony size. In these species values for the larva:worker ratio also varied approximately between 2.0 and 1.0 in colonies with more than ca. 100 workers during the queen rearing period.

Judging from these data, it seems likely that a reduction in the larva:worker ratio to a point below 2.0 with an increase of the worker population which maintains a certain balance in each species is a signal for queen production, though worker population for rearing queen brood differs considerably among *Vespa* species.

## 5. Nest survival

### 1) Survivorship of colonies

In *Vespa* species it is difficult to obtain reasonably accurate estimates of the survivorship of colonies from the time of nest initiation because the density of nests in the field is generally much lower than those

of other Japanese social wasps such as *Polistes* and *Vespula* species.

Only a small amount of data are available on the nest of *V. analis*. From 1964 to 1975, I located 59 nests of this species and observed them from the solitary period: 28 (47.5%) lost their queens before worker emergence, 8 (13.6%) died out during the cooperative period, 3 (5.1%) failed to produce sexuals in spite of their worker production, 2 (3.3%) were destroyed by *V. mandarinia* when they matured, and only 18 (30.5%) survived to produce new queens. These figures show that in *V. analis* a large number of colonies perished during the solitary period mainly because of the loss of their queen.

Table 40 indicates the number of unsuccessful nests in the five *Vespa* species based upon my observation and the analysis of nest contents at the time when the nests were found in the field. The data from such nests give some information with which to estimate the survivorship of *Vespa* colonies, and various factors contributing to colony termination are given in Table 41.

Table 40. The number of unsuccessful nests at each developmental period in five *Vespa* species.

Species	Period						Total
	Solitary*			Cooperative	Polyethic	Reproductive	
	I	II	III				
<i>V. similima</i>	7 (14.2)	4 (8.2)	5 (10.2)	6 (12.2)	7 (14.3)	20 (40.8)	49
<i>V. crabro</i>	3 (10.0)	6 (20.0)	7 (23.3)	9 (30.0)	3 (10.0)	2 (6.7)	30
<i>V. analis</i>	7 (6.8)	12 (11.8)	34 (33.3)	22 (21.6)	14 (13.7)	13 (12.7)	102
<i>V. mandarinia</i>	0 (0.0)	2 (7.4)	5 (18.5)	6 (22.2)	3 (11.1)	11 (40.7)	27
<i>V. tropica</i>	3 (8.1)	5 (13.5)	7 (18.9)	11 (29.7)	7 (18.9)	4 (10.8)	37
Total	20 (8.2)	29 (11.8)	58 (23.7)	54 (22.0)	34 (13.9)	50 (20.4)	245

\* I: before hatching of larvae, II: from hatching of first larvae to spinning of first cocoon, III: thereafter till the emergence of the first worker. Parenthesized figures show % ratio in each period.

In *V. analis* termination of the colony was observed most frequently before worker emergence, which included 51.9% of all unsuccessful nests so far observed. A secondary period of high mortality, the successive cooperative period, resulted in a loss of 21.6%. These cases seem to be approximately similar to the previous data. Such great colony mortality in *V. analis* seems to be mainly caused by the loss of the queen during her foraging periods from the solitary to the cooperative period, and 49.0% out of unsuccessful nests lost their queen either before or soon after first worker emergence.

In colonies of *V. simillima* which often change their nesting site after worker emergence from the original closed place to an open place, 32.6% of all the unsuccessful nests died out during the solitary period before moving from their original nesting site. The highest rate of colony cessation, 40.8% of all the unsuccessful nests, was obtained during the period after the emergence of sexuals. This higher mortality in such matured colonies was mostly brought about by attacks of *V. mandarinia*.

In *V. crabro* 53.3% of the unsuccessful nests failed during the solitary period, and 30.0% in the cooperative period. In both cases colony termination was mostly caused by the loss of the queen, and in the latter case, of 9 nests perishing during the cooperative period, three were caused by the loss of the queen which

Table 41. Factors contributing to colony termination in five *Vespa* species.

Species	<i>anaeth</i>			<i>simillima</i>			<i>crabro</i>			<i>mandarina</i>			<i>tropica</i>			Total		
	A + B			A + B			A + B			A + B			A + B			A + B		
Period	A	B	%	A	B	%	A	B	%	A	B	%	A	B	%	A	B	%
Loss of queen	50	0	50 (49.0)	3	5	8 (16.3)	9	0	9 (30.0)	8	0	8 (30.8)	18	2	20 (54.1)	88	7	95 (38.9)
Natural enemies																		
Attack by honey buzzards	0	11	11 (10.8)	0	0	0 (0.0)	0	0	0 (0.0)	0	0	0 (0.0)	0	0	0 (0.0)	0	11	11 (4.5)
Attack by <i>Vespa mandarina</i>	0	6	6 (5.9)	0	17	17 (34.7)	0	3	3 (10.0)	0	0	0 (0.0)	0	1	1 (2.7)	0	27	27 (11.1)
Styloplazation by <i>Xenos crabro</i>	0	0	0 (0.0)	0	0	0 (0.0)	1	0	1 (3.3)	1	0	1 (3.8)	0	0	0 (0.0)	2	0	2 (0.8)
Parasitism by lepidopteran	0	0	0 (0.0)	0	0	0 (0.0)	0	0	0 (0.0)	0	0	0 (0.0)	0	1	1 (2.7)	0	1	1 (0.4)
Human interference																		
Destruction by man	3	3	6 (5.9)	1	3	4 (8.2)	2	1	3 (10.0)	0	10	10 (38.4)	0	0	0 (0.0)	6	17	23 (9.4)
Effect of insecticide spray	4	2	6 (5.9)	2	1	3 (6.1)	4	0	4 (13.3)	0	0	0 (0.0)	0	2	2 (5.4)	10	5	15 (6.1)
Effect of land reclamation work	0	0	0 (0.0)	0	0	0 (0.0)	0	0	0 (0.0)	0	1	1 (0.0)	0	0	0 (0.0)	0	1	1 (0.4)
Climatic factors																		
Strong wind with heavy precipitation	7	5	12 (11.8)	0	0	0 (0.0)	0	0	0 (0.0)	1	2	3 (11.5)	1	0	1 (2.7)	9	7	16 (6.5)
Unknown factors	11	0	11 (10.8)	16	1	17 (34.7)	9	1	10 (33.3)	3	1	4 (15.4)	7	5	12 (32.4)	46	8	54 (22.0)
Total	75	27	102	22	27	49	25	5	30	13	14	27	26	11	37	161	84	245

\* A: Periods from solitary to cooperative period, B: periods from polyethic to reproductive period. Parenthesized figures show % ratio throughout A + B.

could not locate the new nesting site in a concealed place, as this species also tends to change its nesting site when the nest space becomes too narrow for comb building.

In the case of *V. mandarina* the discovery of nests is very difficult, especially at the earliest stage, because of its exclusive subterranean nidification. The period of greatest colony perishing, resulting in 40.8% of all the unsuccessful nests, was when the nest matured and produced sexuals. After the emergence of sexuals 10 out of 11 nests that had perished had been destroyed by bee keepers who sought the nests because this species causes serious damage to honeybee colonies.

In *V. tropica* 40.5% of all the unsuccessful nests failed during the solitary period and 29.7% in the cooperative period. Of 37 nests, 18 died out due to the disappearance of the queen, probably during foraging.

Judging from these data, in general, the demise of *Vespa* colonies seems to occur very frequently during the solitary period and the cooperative period when the queen still continues to forage outside the nests, though there exist some specific differences.

## 2) Mortality factors

Table 41 also shows mortality factors affecting hornets mainly at the nest level rather than at the individual

level. These factors operate on *Vespa* colonies in a similar way to the "all or none" action reported for aggregations of the immature stages of a stink bug (HOKYO and KIRITANI 1964). Five mortality factors are recognized: (1) disappearance of queen, (2) natural enemies, (3) human interference, (4) climatic factors and (5) unknown causes.

#### (1) Disappearance of queen

From Table 41, it is estimated that the main cause of colony demise in *Vespa* is attributable to the disappearance of the queen, particularly at an early stage of nesting. Among 245 nests of the five *Vespa* species examined, these orphaned nests represented 38.9% of the total unsuccessful nests, though the ratio of nests that lost their queen ranged from 10.0% of unsuccessful nests of *V. crabro* to 54.1% of those of *V. tropica*. There may be some physical or biotic factors which cause the disappearance of founding queens, such as natural enemies, climatic conditions, availability of food, human interference, physiological death, failure to discover new nest sites in nest relocation and evacuation as reported in *Polistes* species (YOSHIIKAWA 1954). I observed that two founding queens of *V. crabro* which had missed their new nests and disappeared, and one of them happened to be killed by the queen and workers of a different nest because she had mistaken it for her own nest site (MATSUURA 1970). However, it is generally impossible to determine the cause of the disappearance of the queens in their foraging trips by direct observation.

The fate of these orphaned nests may be due to one of the following: (1) end of the colony caused by death of the larvae and newly emerged workers in the solitary period, (2) gradual disintegration of the colony caused by successive disappearance of the workers in the cooperative period, (3) production of males by laying workers during and after the cooperative period. In case of (3) the ovarially developed but uninseminated workers produce only males - grandsons of the lost queen. These males may be able to affect the productivity of the next generation by inseminating some new queens when they appear in autumn. The number of such males produced in orphaned nests is often much more than that of normal nests at the corresponding period.

#### (2) Natural enemies

There are four natural enemies which are regarded as mortality factors operating at the colony level, not at the individual level. These are "colony predators" such as the congeneric species, *V. mandarinia* and the honey buzzard, *Pernis apivorus*, L.

*V. mandarinia* attacks nests of other congeneric species. Once discovering a nest, several dozens of *V. mandarinia* workers visit it and a colony is almost completely destroyed in a few days. The attack is seasonally well delimited and catastrophic damage always occurs from mid-August to early November, when the nest reach their maximum size with sexuals. This strong predation by *V. mandarinia* caused the death of the highest proportion of all the unsuccessful nests at the mature stage. It is noteworthy that the percentage of *V. simillima* in particular is higher than that of any other species except for *Vespula flaviceps* (Table 20). It seems likely that *V. simillima* is destroyed frequently because their nests are abundant in the district surveyed; also their nests are built in the open and in conspicuous places such as under the eaves of buildings. The colony size may also play a significant role in the preference of *V. mandarinia* for *V. simillima* because the nest of the latter is much larger than that of any other congeneric species.

The honey buzzard, *Pernis apivorus*, is known as a predator of *Vespula* colonies in European countries (SCHREMMER 1962, TRAP-LIND 1962, EDWARDS 1980). This buzzard is not very common in the regions surveyed, and its attack on *Vespa* species was limited to the colonies of *V. analis*. Of 27 nests in *V. analis* which died out during and after the polyethic period, at least 11 were considered to have been destroyed by this buzzard. At a nest of this buzzard I often observed that the birds brought parts of a comb into the nest, though it was not determined whether the buzzard had preyed on adult hornets or not. Once the buzzard discovers hornets' nest, it keeps visiting it and plunders the remaining comb until the colony is completely broken up. A nest attacked by the buzzard could be easily distinguished by the lack of combs inside the envelope. It is not certain that the buzzard has a specific preference for the nest of *V. analis*; rather this species may be utilized because of the relatively mild nature of its counter-attacks when disturbed, although I have never seen an actual attack. The exclusively aerial nests, too, are probably easily discovered by the buzzard.

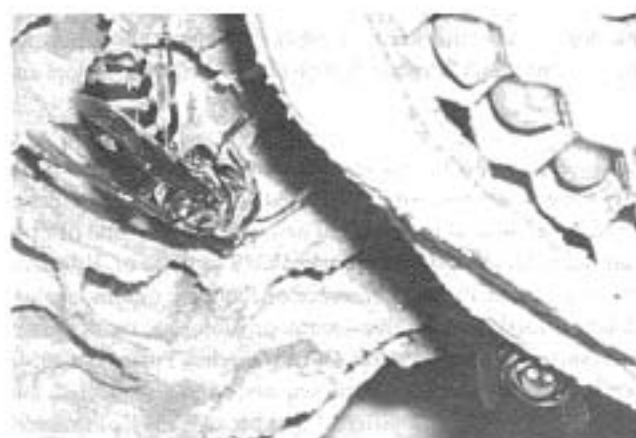


Fig. 82. Styloped workers of *Vespa crabro* on the envelope.

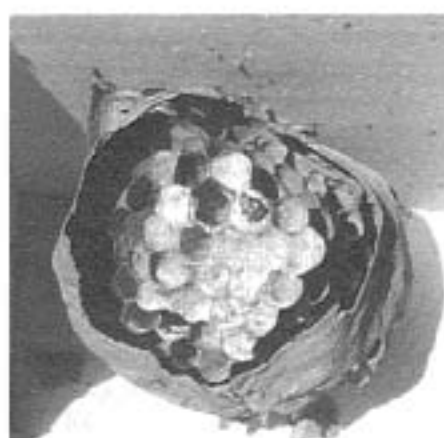


Fig. 83. Nest of *Vespa tropica* attacked by a lepidopteran, *Pyrallis regalis*.

*V. simillima* is one of the commonest species, as already stated, but the buzzard may keep away from its nests because of its huge colony size and resultant severe counter-attacks by many more workers than the case of *V. analis*.

A strepsipteran, *Xenos crabronis* Pierce, is occasionally found as a parasite within adult hornets (Fig. 82). The styloped hornets spend most of their time resting on the comb within the nest without doing any tasks, particularly extranidal activities, and after about two weeks they leave but do not return to their nest. The level of parasitism of styloped hornets is usually very low in mature colonies: I found only 1.3% of styloped *Vespa* workers in a total of 245,352 adults examined, and the effect of a strepsipteran is probably negligible in regulating *Vespa* colonies. In the early stage of nesting, however, the parasitism often reached a high level. Two colonies each of *V. mandarinia* and *V. crabro* were destroyed because all the workers emerging in the cooperative period were styloped by *Xenos crabronis* and they left their nest without returning.

I have never found *Vespa* nests containing lepidopterous larvae during their active season, excepting the one record shown in Table 41. On this occasion it was observed that several dozens of the larvae of *Pyrallis regalis* Boisduval in the cells of *V. tropica* had been feeding on the larvae and pupae in September 1970 and had destroyed both brood and the nest fabric (Fig. 83), despite the presence of several worker hornets.

### (3) Human interference

In Japan *Vespa* hornets are generally considered a pest to be feared, with extreme nuisance value and potential health hazard caused by stinging. This attitude exists among most people in all localities where *Vespa* species occur, and some of them attempt to destroy their nests whenever they find them. To most Japanese apiarists, on the other hand, *V. mandarinia* is a serious pest causing catastrophic damage to honeybee colonies. So they search for the nests of this species by following the flight path of worker hornets. The destructions of nests by man plays a more important part in colony mortality of *V. mandarinia* compared to the other four species, and destruction by apiarists accounted for 38.4% of all the unsuccessful nests: most of them were killed in the later stage of nesting.

A wide variety of insecticides seems to be extremely toxic to both *Vespa* larvae and adults. Some, such as carbaryl, dimethoate, diazinon, etc., which are adopted in agricultural spray programs for pest control in orchards, cause significant mortality if sprayed near their nests. Many foraging hornets, both queens and workers, die when poisoned directly with such insecticides in the field. Some of them contact residues in the field and carry contaminated water and food back to their nest. These cause the death of newly



emerged hornets as well as foragers through trophallaxis. Such hornets move about on and near the ground by their nest but are unable to fly and take two to three days to die. Brood is mainly killed by chilling or starvation due to the lack of feeding hornets. The level of accidental killing of colonies through the use of insecticides is estimated at 6.1% of the total of the five species, but some of the causes of disappearance of queens in foraging may also be attributable to the effect of insecticides.

(4) Climatic factors

Weather conditions as direct mortality factors appears to be unimportant to *Vespa* colonies under normal conditions. However, strong wind with heavy precipitation often blew off *V. analis* nests which were attached to trees in the early stages of colony growth. In general, nests of *V. analis* in the early stages are much more susceptible than nests in the later stages to the action of storms because the former are more fragile in structure than the latter which are rigidly connected with twigs around the nest. In fact I have never found examples of *V. analis* nests which were damaged or destroyed by storm or typhoon in the later stage of nesting after September, similarly in aerial nests of *V. simillima*. For species of subterranean or closed nidification such as *V. mandarinia* and *V. tropica* heavy rainfall occasionally caused the destruction of their nest, though a few nests of *V. mandarinia* and *V. tropica* were destroyed as a direct result of flooding.

(5) Unknown factors:

The last line of Table 41 shows that unknown factors account for high proportions of terminated nests of *Vespa* species throughout their active seasons, though a part of them may be attributable to one of the factors mentioned above.

## 6. Annual fluctuations in the number of *Vespa* colonies

Table 42 shows the number of mature *Vespa* colonies collected during a 12-year period in and near Kibi.

Table 42. Fluctuations in the number of mature nests in five *Vespa* species collected in and near Kibi, 1964 - 1975.

Year	<i>simillima</i>	<i>crabro</i>	<i>analis</i>	<i>mandarinia</i>	<i>tropica</i>	Total
1964	10	4	8	2	2	26
1965	10	6	12	3	2	33
1966	9	5	2	6	1	23
1967	9	5	19	8	2	43
1968	13	5	17	3	6	44
1969	9	0	3	2	2	16
1970	25	4	1	2	2	34
1971	23	3	7	7	6	46
1972	26	3	13	4	2	48
1973	16	7	15	2	5	46
1974	6	7	3	4	1	21
1975	10	8	19	2	4	43
Total	166	57	119	46	35	423

These data can not be used to directly compare interspecific differences in nest numbers at the study area, but the figures may provide a relative index to monitor inter-specific relative abundances.

The higher rank of both *V. simillima* and *V. analis* may reflect their aerial nests which are easily discovered, while the lower abundance of the other three species may be related to their concealed nidification. The relative abundance among these five species estimated by several methods in and near Kibi are ordered approximately as follows:

Visits to apiaries: *mandarinia* > *simillima* > *crabro* > *analis* > *tropica*

Visits to tree sap sources: *mandarinia* > *crabro* > *analis* > *tropica* > *simillima*



Visits to houses: *tropica* > *crabro* > *mandarinia* > *simillima* > *mandarinia*

General extranidal activities: *mandarinia* > *tropica* > *analis* > *crabro* > *simillima*

Discovery of hibernating queens: *analis* > *tropica* > *simillima* > *mandarinia* > *crabro*

Nest discovery: *simillima* > *analis* > *crabro* > *mandarinia* > *tropica*

The marked discrepancies among these different crude estimates show how difficult it is to accurately estimate the relative abundance of species in a group such as *Vespa*, with a wide flight radius and relatively low density.

It is possible that we may estimate the number of almost all of the completed nests of *V. simillima* in a defined area by searching all their most likely nesting places at the end of the season. Table 43 shows such

Table 43. Fluctuations in the number of nests of *Vespa simillima* in four adjacent areas covering 300 ha, near Kibi-cho, 1964-1975.

Sub-areas	Area(ha)	Year												Total
		'64	'65	'66	'67	'68	'69	'70	'71	'72	'73	'74	'75	
A. Mutsugawa in Kanaya-cho	75	1	1	3	3	2	1	2	3	1	0	1	1	19
B. Yoshikawa in Kanaya-cho	80	2	1	2	1	2	3	4	1	2	2	1	2	23
C. Yoshimi in Kibi-cho	50	2	0	2	4	1	0	2	2	1	1	0	1	16
D. Yamada in Yusa-cho	95	0	1	3	1	1	0	2	3	1	1	2	2	17
Total no. nests observed		5	3	10	9	6	4	10	9	5	4	4	6	75
No. nests/ha.	300	0.02	0.01	0.03	0.03	0.02	0.02	0.03	0.03	0.02	0.02	0.02	0.02	
No. of cells per colony*	Minimum	2,381	3,263	3,053	3,504	3,418	2,500	1,885	2,572	4,802	3,438	2,949	2,988	
	Maximum	10,058	9,323	8,656	8,433	7,980	8,656	9,936	8,465	6,873	9,602	8,744	7,444	
	Average	6,313	6,173	5,844	5,899	4,325	5,124	4,666	5,211	5,106	6,322	5,450	6,708	

\* All the nests were taken after cessation of nesting activities.

a record of the density of *V. simillima* nests surveyed in four adjacent areas near Kibi, where the number of the nests of this species is fairly high. The number of nests per year varied only 3.33 times from the minimum to the maximum, during the 12 years. Such a small range of fluctuations of nests means that this species is strongly controlled by natural stabilizing mechanisms regulating the populations at low levels, despite the fact that these colonies are estimated to have produced a total of 1,800-6,000 new queens every year.

## 7. Discussion

### 1) Survivorship curves

In his comparative review on survivorship curves for various insects, Irô (1959) suggested that brood mortality decreases as parental care increases and the survivorship curves tend to be convex. Very low mortality at the brood stage has so far been confirmed by several workers in a few social wasps and bees. SPRADBERY (1973) showed an estimated brood mortality of 3.5% in workers of *Vespula germanica*. In the honeybee, *Apis mellifera*, which has achieved highly developed social care the survivorship curve is of the convex type, which is very similar to that of man, and the mortality of brood stages is 14.9% under favourable conditions (FUKUDA and SAKAGAMI 1968, SAKAGAMI and FUKUDA 1968). They pointed out that the conditions necessary for brood survival in normal colonies of the honeybee are kept within the optimal range by the adult workers, resulting in a very low mortality.

The results obtained from the five *Vespa* species obviously confirms this. However, the very low mortality rate in brood developmental stages of workers is achieved only under favourable conditions. In such

colonies mortality factors operating on the brood are very few except for cannibalism by the adult workers, because there are few natural enemies able to attack them individually in their nest. On the other hand, nursing adult sexuals during the reproductive period evokes a catastrophic brood mortality, even in favourable colonies, which is probably caused by a decrease in attention given to the brood.

There are essentially two mortality factors operating at this period, i.e., cannibalism by adult hornets and starvation. The former is literally a part of the colony 'feed back' system as the means to retaining protein food supply when foraging workers change their main food collection from protein for the larvae to carbohydrate for adult sexuals. In this way workers utilize the brood as their protein food. With reduced feeding, most of the larvae remain in the last instar, though they continue to supply granular secretion which is frequently taken by adult hornets, and such circumstances obviously accelerate starvation of the brood. Finally, the brood during the later stage of the colony cycle are destined to be abortive ones in temperate regions, as already pointed in *Polistes* wasps (MATSUURA 1977).

Compared with the low mortality of worker brood in normal colonies the mortality rate of the adult stage is compensatingly high with the commencement of their foraging activities. ISHAY et al. (1967) noticed the lower life span in workers of *Vespa orientalis* having access to the field and reported that during the first 14 days of adult life, the workers suffered a mortality of 8.8% in confined to the nest and 42.5% if allowed to forage outside. In honeybees, *Apis mellifera*, which do not normally begin foraging until the tenth day or later, mortality is also very high when they begin leaving the hive on foraging trips (SEKIUCHI and SAKAGAMI 1966, SAKAGAMI and FUKUDA 1968). According to FUKUDA and SEKIUCHI (1966), mortality factors of honeybee workers during the foraging period are divided into three components, ecological hazards, physiological consumption due to intense foraging and that due to intense brood rearing during the earlier adult stages, though it is impossible to separate them.

In *Vespa*, workers start to leave the nest on foraging trips two or three days after their emergence, and continue their foraging activities usually until their last day alive, though it is reported that no workers of *V. orientalis* leave the nest after an age of 35-38 days (ISHAY et al. 1967). Most of the foraging workers are considered to die from ecological hazards, such as predation or eventual accidents, and those which have not encountered such misfortunes would die of physiological senescence, though it is very difficult to measure quantitatively the effect of such factors on the mortality by direct observation.

It seems likely that the longevity of life span in *Vespa* workers is closely related to the size of population in such a way that the longer the life span of adults the smaller is the colony size attained. It should be noted that the life span of the workers of *V. tropica*, which has the smallest colony size and the shortest activity period in the Japanese *Vespa*, is remarkably long as compared to that of the other four species.

Finally it must be emphasized that in *Vespa* species the mortality factors affecting each individual in a colony differ essentially from those which operate at the colony level: the latter often cause catastrophic damage to all the colony.

## 2) Seasonal changes in population structure

The seasonal changes in the population structure of vespine colonies have been discussed by many workers (JANET 1895, BODENHEIMER 1937, ISHAY 1965, ISHAY et al. 1965, MACDONALD et al. 1974, ROUSH and AKRE 1978, ARCHER 1982). LÖVGREN (1958) constructed a mathematical model measuring the seasonal growth and productivity of wasp colonies, using parameters based on *Vespula* species, taken from RICHARDS and RICHARDS (1951). SPRADBERY (1971) exemplified Lövgren's model in *Vespula* species and provided much better estimates of the parameters for *Vespula* colonies. ARCHER (1972, 1981) also gave an account of the seasonal development of *Vespula* colonies in relation to characteristics of colony members.

The general pattern of seasonal colony development in *Vespa* is characterized by slow development in the early stage (MATSUURA 1973), followed by explosive development in the later stage and then the rapid and terminal decline after sexuals have been produced. This is similar to that of many species of temperate polistine and vespine wasps (JANET 1895, 1903, SPIETH 1948, YOSHIKAWA 1962). Concerning the general pattern of the colony development, no marked variation exists among the Japanese *Vespa* species, but some specific difference are recognized (Fig. 65). That principal differences are as follows: (1) duration

of colony cycles, (2) attainable size of the mature colony, (3) time of the emergence of sexuals. Comparing the duration of colony cycles, the colonial life of *V. tropica* is about 3.5 to 4 months, which is the shortest among the Japanese *Vespa* species, while that of *V. simillima* is nearly twice as long at 7 to 7.5 months. The other three species occupy places between the two extremes in the following order: *simillima-mandarinia-analis-crabro-tropica*. As overwintered queens of every species, except for *V. tropica*, begin to build their nests at about the same time during mid- to late May, the differences could result from the fact that the long-cycle species generally need more time in order for the colony to mature, and attainable colony size is partly but necessarily linked with the duration of colony cycles in such a way that the larger the typical colony size the longer the colony cycle is prolonged. A similar trend is reported in *Vespula* and *Dolichovespula* species (MACDONALD et al. 1974, GREENE 1979) and *Polistes* species (MATSUURA 1975). *V. tropica* which is the very short-cycle species has the smallest colony size among the Japanese *Vespa* species. On the other hand, *V. simillima* which is long-lived develops enormous colonies, as large as those of some *Vespula* species (MATSUURA 1980, YAMANE et al. 1980). The colony size of *V. crabro* and *V. mandarinia* is medium among the five *Vespa* species: the number of cells in the largest colony in each species is about 4,500, although *V. crabro* colonies are generally smaller than *V. mandarinia* colonies. The duration of colonial life is much shorter for *V. crabro* than for *V. mandarinia*: the end of the colony in the former species occurs in mid- to late October whereas it extends to late November in the latter species. The colony of *V. analis* is much smaller than any other *Vespa* species except for *V. tropica*, but the increase in number of cells is very small during the active period, though this species is rather long-lived.

Sexual production always occurs at the end of colony development, so the time of emergence of sexuals is closely related to the time of colony termination in each species. New queens emerge from early September to late November in the following order: *tropica-crabro-analis-simillima-mandarinia*. Just prior to the production of new queens, the larva:worker ratio is considerably reduced and drops to its lowest level, below about 2.0 in each *Vespa* species. Such a decrease in the larva:worker ratio is commonly recognized in social wasps and bees as one of the most significant cyclic changes at queen rearing time (RICHARDS 1946, SPRADBERY 1965, 1971, ARCHER 1972). The decrease in the larva:worker ratio indicates an approach to a suitable condition for queen production. POTTER (1965) suggested in *Vespula* that a major contribution to the decrease in the larva:worker ratio resulted from the marked increase in worker longevity at the later stage of nesting.

On the other hand, the minimum number of workers in a mature colony which is regarded as necessary to succeed in producing new queens varies considerably among the species. For example, in *V. tropica* new queens can be produced in a colony with more than ca. 20 workers, while in most colonies of *V. simillima*

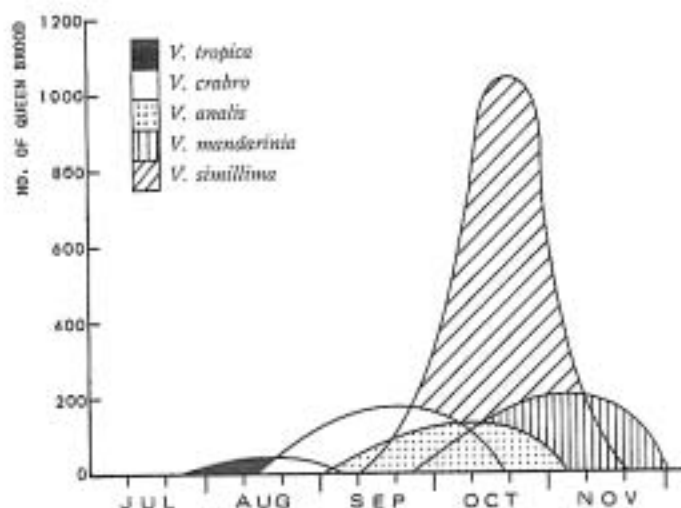


Fig. 84. Schematic representation of the rearing time of new queens in the five *Vespa* species.

the number of workers present in a reproductively successful colony needs to be at least ca. 300 workers. Furthermore, it is clear that the larger the colony size, the more sexuals are produced, though correlation between colony size and the number of new queens produced in the congeneric species is not markedly obvious except for *V. simillima*.

Recently, ARCHER (1980) pointed out the existence of an alternative strategy in colony development in British social wasps: 'long-cycle' as typified by *Vespula vulgaris* and 'short-cycle', e.g. *Dolichovespula sylvestris*, and discussed the characteristics and the evolutionary significance of the two strategies by using a computer model. In the case of the Japanese *Vespa* species it is recognized that there is every gradation of colony cycle from 'short-cycle species' with a small colony, e.g. *V. tropica*, 'long-cycle species' with a large colony size, e.g. *V. simillima*. The other three species, *V. crabro*, *V. analis* and *V. mandarinia* have an intermediate-cycle, but occupy different positions between the two extremes. Consequently it seems likely that the rearing time of new queen larvae is somewhat different in each species (Fig. 84) as pointed out in European wasps by ARCHER (1980). As mentioned in chap. III, the five *Vespa* species have somewhat different requirements for sources of food, especially protein. Therefore, the difference in the length of the colony may be reflected partly in the difference of food sources, and the five *Vespa* species probably reduce competitive overlap with each other for food sources. This results in their occupying different niches.

### 3) Mortality factors at colony level

It has been emphasized that most mortality in temperate social wasps occurs in the solitary period as reported in *Polistes* spp. (YOSHIKAWA 1954, YAMANE and KAWAMACHI 1975, MATSUURA 1977, MIYANO 1980), in *Vespula* spp. and *Dolichovespula* spp. (DUNCAN 1939, SCOTT 1944, BRIAN and BRIAN 1948, 1952). In the colonies of *Polistes*, colony failure rate in the solitary period is variable from 42.6% (MIYANO 1980) to 84.2% (YOSHIKAWA 1954) by different local environments. YOSHIKAWA (1954) inferred that these failures were mostly due to loss of the foundress. On the other hand, BRIAN and BRIAN (1952) and ARCHER (1980) noticed that in *Dolichovespula sylvestris* colonies, most seem to fail on account of some apparent weakness of the queen.

As to *Vespa* hornets the data on the unsuccessful nests observed in the field showed that the colony failure rate in the three species, *V. analis*, *V. crabro* and *V. tropica*, during the solitary period was remarkably high in comparison with that of the other two species, *V. mandarinia* and *V. simillima*. As pointed out previously, however, the chances of finding the incipient nests of *V. tropica* were very small because of its covered nidification in addition to the primary low density. Thus, it seems likely that there exist many more nests of this species which have died out at the incipient stage without discovery. It is probable that similarly heavy early mortality during the solitary period occurs among all these five species. Data for nest survival indicate the high frequency of nest demise occurs during the cooperative period as well as at the solitary period, and the main factor for colony failure could be attributable to the disappearance of the queen during her foraging trips though it is impossible to estimate the cause of this disappearance in detail. Once reaching the later part of the cooperative period in which the queen does not forage outside the nest, her mortality probably decreases because of liberation from foraging tasks with high risk. After the polyethic period, colony mortality decreases markedly as the colony becomes established and strong against invaders. Nevertheless, a high rate of colony destruction occurred in the mature nests of both *V. simillima* and *V. mandarinia* in comparison with those of other *Vespa* species in spite of their formidable ability to attack and to conquer other animals. It is remarkable that the most mortality occurs by attack of *V. mandarinia* in the case of *V. simillima* and by destruction by men in the case of *V. mandarinia*, and these play an important part as regulating factors.

It should be pointed out that *Vespa* colonies seems to remain at a fairly low level of abundance in at least southwestern Japan, in spite of their high productivity. In the case of *V. simillima* which can produce more than 1,000 queens per colony, a high rate of reproduction would require a mortality of more than 99.9% to maintain the same numbers of colonies which reach the reproductive period. In other words, at the most only a few queens would be expected to survive to maturity in a stable population of colonies in an area. The same tendency is reported in *Vespula* wasps, too, and it is suggested that most mortality



occurs before nests are built or during the period of colony initiation (BRIAN 1965, SPRADBERY 1973, ARCHER 1980). Therefore, it is assumed that there must exist a heavy mortality of *Vespa* queens which may occur during the period from the dispersal of new queens from the parent nest to the founding of new colonies in spring. Possible factors affecting small vespine populations such as *Vespa* and *Dolichovespula* have been discussed, especially climatic factors (LATTER 1985, BEIRNE 1944, FOX WILSON 1946, DÖHRING 1960). These observations indicated that the meteorological conditions did not play a dominant role in queen control, but they all considered that spring weather was important as a factor in queen control.

Factors such as natural enemies, physiological death, etc. may cause a loss of hibernating queens to a certain extent. However, the cause of death of the bulk of queens of vespine species remains uncertain as was discussed for *Vespa* spp. (SPRADBERY 1973, ARCHER 1980), though intra- and interspecific competition among queens for nest sites in spring is likely to be one of the most significant factors in population regulation, especially during years of abundant queens, leading to usurpation (NIXON 1936, BRIAN and BRIAN 1952, MATSUURA 1970, SPRADBERY 1973). ARCHER (1980) suggested the existence of self-regulating mechanisms in *Vespa vulgaris* which caused a two-year cycle of wasp abundance and scarcity in England. He pointed out that a link between queen quality and competition for nest sites in spring plays the most important role as a likely self-regulating factor. The number of mature colonies in *Vespa* species was relatively constant irrespective of their high production of new queens as compared with violent fluctuation in numbers of *Vespa* colonies, which show a 10-42-fold difference between the extremes of scarce and abundant years (NICHOLSON 1921, BEIRNE 1944, FOX WILSON 1946, EDWARDS 1974, 1979, ARCHER 1980).

In this section I have discussed mainly the loss of colonies in *Vespa* and referred only to those colonies which have passed their vulnerable incipient solitary period. However, it is probable that there exist stabilizing mechanisms for the entire population of *Vespa* species. To understand this it is of great importance that an accurate estimate of the new queens in the six-months non-nesting period, though there is little information on this subject.

## VI. GENERAL DISCUSSION

The subfamily Vespinae, certainly occupying a summit of vespid evolution, contains only four genera: *Provespa*, *Dolichovespula*, *Vespa* and *Vespa*.

The first genus is considered to be the most primitive, and the three known species occur only in Southeast Asia (VECHT 1936, 1957). The most significant behavioural characters of this genus summarized in my recent work in Sumatra (MATSUURA, unpub.) are: (1) typically nocturnal activity, (2) nest foundation by swarming with a single queen and several dozens of workers, (3) very low numbers of queens produced (< 20 queens per colony), (4) low values for the larva:worker ratio at any point in the colony cycle (< 3.0), (5) heterogeneous queen production on a single comb, (6) special queen-rearing cells with extremely prolonged cell walls, (7) tree branch nidification, (8) the tough and comparatively pliable nest with a complete envelope consisting of a few felt-like layers on the top surface and numerous small scalloped structures in the upper half, and several layers of smooth, broad overlapping carton on the lower half in a matrix of dense, rigid carton, (9) feeble cell wall scraping by mature larvae, (10) presence of a distinct royal court of workers, surrounding the queen, (11) irregular distribution of brood on a comb caused by utilization of the same cell several times, (12) multiple utilization in the same queen cells, (13) strictly predacious, carrion not utilized, (14) long colony duration (7-10 months), but not perennial, (15) rather large colony size (ca. 1,500 workers and ca. 5,000 cells at peak in *Provespa nocturna*), (16) presence of flying ability in the queen throughout her lifetime. Some of these characters, especially 2, 8 and 14 can be regarded as adaptations to environmental factors of tropical regions: seasonality and natural enemies. The swarming mode of colony foundation is almost exclusively tropical, and some peculiarities of nesting biology enumerated above, especially 3-5, 15 and 16, appear to be connected with the mode of colony founding. This habit is interpreted as an adaptation to a high level of ant predation (JEANNE 1975). On the other hand, the descriptions given above, especially

1 and 8, suggest some bionomic characters, specific to this genus, which are of some interest for the nocturnal activities, like *Apoica* in South America (RICHARDS and RICHARDS 1951). These behavioural characters as indicators of vespine phylogeny show that this small group is adapted for living in tropical regions as the most specialized group among the Vespinae.

Both *Vespa* and *Dolichovespula* are distributed in the northern hemisphere with a complete adaptation to temperate regions and are not found in tropical regions. Comparing the two genera, *Vespa* and *Dolichovespula*, it is asserted that the former as a group is more advanced than the latter in some characteristics, though the complex is monophyletic with the ancestors of the genera probably evolving from *Vespa* stock (VEICHT 1957, RICHARDS 1971, YAMANE 1976). Some specific and generic differences between them are pointed out in Table 44, based upon data from the Japanese species, though comparative biology of both genera

Table 44. Species groups and some biological characteristics of the two genera, *Vespa* and *Dolichovespula* in Japan (MATSUURA 1981 and unpub. data).

	<i>Dolichovespula</i>		<i>Vespa</i>			
	<i>scoring/colden and japonica</i>	<i>media</i>	<i>flaviceps</i>	<i>shibei</i>	<i>vulgaris</i>	<i>schrenckii</i>
Nest sites	usually aerial, sometimes protected or subterranean	always aerial	usually subterranean, sometimes protected or aerial			usually subterranean, sometimes protected
No. of cells at peak	500 - 1,500	500 - 1,200	3,000 - 17,000	5,000 - 17,000	3,000 - 10,000	300 - 2,500
Approximate colony duration (months)	3.5 - 4.0	4.0 - 5.5	8.0 - 9.0	8.0 - 9.0	6.0 - 7.5	4.0 - 5.5
Decline	mid-Aug. to mid-Sep.	mid-Aug. to mid-Sep.	late Sep. to early Dec.	late Sep. to early Dec.	mid-Sep. to late Oct.	early Sep. to mid-Oct.
No. of new queens produced per colony	30 - 120	30 - 150	400 - 1,500	500 - 2,500	300 - 1,000	50 - 400
Queen nest						
Pedioel	twisted with a hanging short	twisted with a hanging short	twisted with a hanging short	twisted with a hanging short	twisted with a hanging short	twisted with a hanging short
A disc above the comb*	absent	absent	present	present	present	present
Envelope	laminar and pliable	laminar and pliable	laminar and fragile	laminar and fragile	laminar and fragile	laminar and pliable
Major nest suspensoria	barrenlike	barrenlike	cordlike	cordlike	cordlike	both types present
Envelope	laminar and pliable	laminar and pliable	scalloped and fragile	scalloped and fragile	scalloped and fragile	laminar and pliable
Prey diversity	strictly predators	strictly predators	predators plus scavengers	predators plus scavengers	predators plus scavengers	strictly predators

\* after YAMANE and MAKINO (1981)

has not yet been studied in detail. In general, members of *Vespa* except for *Vespa schrenckii* have larger colonies with a longer colony duration, and have developed an omnivorous habit, whereas members of *Dolichovespula* and *Vespa schrenckii* have small colonies with a short colony duration, and are usually considered to be strictly predators. It seems likely that in these groups, the colony size attained at peak is linked both with colony life span and prey diversity.

Similar generic characteristics including those of the *Vespa rufa* group are reported from the North American species (DUNCAN 1939, ROUSH and AKRE 1978, GREENE 1979, AKRE et al., 1981) and the European species (KEMPER



and DÖHRING 1962, SPRADBERY 1973, EDWARDS 1980, ARCHER 1980, 1981). ARCHER (1980, 1981) stressed that the strategies between them reflect basic intrinsic differences mainly of a generic origin, and the development of long and short cycle species would reduce competition by allowing the peak colonial populations of long and short cycle species to appear at different times of the year so that possible competition between them, e.g. for food resources, would be reduced although each species, in turn, would exploit that resource. Possibly his interpretation is useful in explaining the evolution of colony characteristics between the two genera, though reference is not made concerning the prey diversity between them. Of particular interest is that in both genera some species lead a permanent social parasitic life. In the case of the Japanese species, *Vespula austriaca* and *Dolichovespula adulterina* do not possess a worker caste but are dependent upon host workers of *V. schrenckii* and *D. norvegicoides* respectively, to rear their brood of sexuals.

The last genus, *Vespa*, has several species in tropical regions but the greatest number of species, as well as the greatest diversity in characters are found in the eastern Himalayas and southern China and these areas are regarded as the original centre of this genus (VECHT 1957). Some of the species are found to be dominant in temperate regions, decreasing in number of species towards the northern and western limits of distribution, in contrast to that of *Vespula* and *Dolichovespula* in eastern Asia (YAMANE et al. 1980). In Japan both the genera *Vespula* and *Dolichovespula* are more boreal or live mainly in high altitudes, in general distribution, whereas *Vespa* are rare or absent in high altitudes, and the five closely related species, which are treated in the present paper, commonly coexist in low mountains and forests and occupy the top ranks among insects and other small animals in southwest Japan.

It is of particular interest how these five species have attained a stable co-existence. The most likely modifications or adaptations in niche exploitation are as follows. First, these five species differ from each other in nesting site as they are classified into the open place and covered place types. *V. analis* and *V. simillima* belong to the former type while *V. simillima* choose some sites, typical of the latter type. *V. tropica* and *V. crabro* prefer to nest only in restricted cavities or in ample spaces both above and underground, whereas *V. mandarinia* is exclusively subterranean. These differences are very subtle to avoid a competitive displacement and have evolved a variety of specializations in nest architecture and modifications of the nest site, such as relocation of nests performed by both *V. simillima* and *V. crabro*.

Secondarily, the five *Vespa* species have achieved a co-existence in their feeding relationships by significant differences among them in such a way as to be either highly specialized or very generalized in their food preferences. *V. tropica* has evolved to specialize only on the brood of the polistine wasps, which are high quality food sources. However, this strategy is presumably only profitable to the species of the small population type such as *V. tropica*, not requiring a large quantity of animal diet. On the other hand, *V. crabro* is a semi-specialist which is highly specialized behaviourally for utilizing any cicada, while keeping an ability to hunt a wide variety of insects when the preferred food source is restricted in density. Both *V. analis* and *V. simillima* are non-specialists utilizing many kinds of live insects and spiders, though there seems to exist some specific preferences. In these two species competition for resources is reduced at least in part by the fact that *V. analis* breed sexuals earlier than *V. simillima*, in addition to the distribution of scattered food sources and their long foraging distance (1–4 km) flight radius in both species (MATSUURA unpub.). *V. mandarinia*, while keeping its polyphagous habit, evolved a specialized way to attack in mass the colonies of social bees and other wasps, including those of congeneric species. This results in a displacement of the ecological niches between *V. mandarinia* and other congeneric species in such a way that *V. mandarinia* affects them in two ways; as a competitor in seeking common food sources and as a predator, being the most important natural enemy at the colony level. *V. mandarinia* owes its success in the strategy not only to its large body and colony sizes, but also to efficient group predation, which is the only case of group foraging in social wasps thus far known. Thus, these differences in food preference among the five species result in reduced competition for food and in utilizing these sources at slightly different times of the year. Each species reaches its greatest need for protein food to coincide with the occurrence of its prey so that competition is effectively eliminated. Therefore, it is suggested that the rearing time of the sexuals, which need the greatest quantity of foods to feed them, is segregated not only by seasonal time but also by length of colony cycle as shown schematically in Fig. 84.

The principal differences are: *V. tropica* is a short-cycle species with the smallest colony size, whereas *V. simillima* is a long-cycle species with the largest colony size. The other species, *V. crabro*, *V. analis* and *V. mandarinia*, occupy intermediate positions between the two extremes both in the length of colony cycle and colony size.

Thus, the five *Vespa* species seem to occupy ecologically different niches in such areas (Table 45) as nest site, feeding habits and colony cycle, which they have coexisted thus far permit coexistence in southwestern Japan.

Table 45. Interspecific ranking among the five Japanese *Vespa* species.

Feature	Species				
	<i>simillima</i>	<i>analis</i>	<i>crabro</i>	<i>mandarinia</i>	<i>tropica</i>
Number of nests studied	1	2	3	4	5
First appearance of queens in spring	1	4	2	2	5
First emergence of workers	1	3	2	4	5
Nest leaving by new queens	4	3	2	5	1
First death of founding queens	5	3	2	4	1
Disintegration of colonies	4	3	2	4	1
Size of cells	5	4	3	1	2
Maximum number of cells in nest	1	4	3	2	5
Number of sexuals per colony	1	4	3	2	5
Aggressiveness towards man	2	4	3	1	5
Interspecific dominance	4	2	3	1	5
Abundance measured by:					
a) visits to apiaries	2	4	3	1	5
b) visits to tree sap sources	5	3	2	1	4
c) visits to houses	4	5	2	3	1
d) general extranidal activities	5	3	4	1	2
e) discovery of hibernating queens	3	1	5	4	2
f) nest discovery	1	2	3	4	5

## SUMMARY

The present study aims to clarify the specific difference in bionomic characters of the five Japanese *Vespa* species, *V. simillima xanthoptera* CAMERON, *V. analis insularis* DALLA TORRE, *V. crabro flavofasciata* CAMERON, *V. mandarinia japonica* RADOSZKOWSKI and *V. tropica pulchra* BUYSSON, which coexist in low mountain areas of southwest Japan. The life history, nesting habits, feeding habits, division of labour and population dynamics, are described primarily by comparing them with each other. The field work was mainly carried out in and near Kibi-cho, Wakayama, southern Japan during the period from 1964 to 1975. A total of 622 nests was observed in and near the study area, and consisted of 288 nests of *V. simillima*, 164 of *V. analis*, 80 of *V. crabro*, 56 of *V. mandarinia* and 34 of *V. tropica*. Results obtained are as follows:

- 1) The annual life cycle of the five *Vespa* species consists of the following six periods, though a little variation in details of the cycle occurs among them: (1) pre-nesting, (2) solitary, (3) cooperative, (4) polyethic, (5) reproductive and (6) hibernating period. Hibernated queens come out from their hibernacula during the period from early April to early June in the following order: *simillima* - *mandarinia* = *crabro* - *analis* - *tropica*. All of the species found their colonies with a single queen which constructs an average of 35 - 40 cells and rears 10 - 15 larvae up to the pupal stage by herself. The first workers emerge from June to July in the following order with a difference of 5 - 6 weeks in peak dates between *V. simillima* and *V. tropica*: *simillima* - *crabro* - *analis* - *mandarinia* - *tropica*. The queens are still involved with both extranidal and intranidal activities for a while after worker emergence. This cooperative period lasts for 2 - 8 weeks and its length is inversely related to the typical colony size. As the number of workers increases, the queens of all species, other than *V. tropica* become restricted to oviposition, leaving all the other tasks to the workers.

This expansive stage lasted until the time when sexuals are produced and the duration of the reproductive period lasts about a month in each species. The disintegration of the colony ordinarily takes place from early September to late November in the following order: *tropica* - *crabro* - *analis* - *mandarinia* - *simillima*. The queens hibernates singly in hibernating spaces within the soil or rotten wood.

- 2) Nest site preference is classified into the open place and concealed place types. *V. analis* and *V. simillima* belong to the former and *V. tropica*, *V. crabro* and *V. mandarinia* to the latter. The queens of *V. simillima* and *V. crabro* tend to initiate their nests in narrow, covered places or underground cavities. When the nest become too large after the emergence of workers, the whole colony moves a new, more spacious site.
- 3) The shape of the completed queen nest was divided into the three types: bowl-shaped (*V. tropica* and *V. mandarinia*), ball-shaped (*V. crabro* and *V. simillima*) and flask-shaped (*V. analis*). The general shape of mature nests varies between the species of the open preference and those of the concealed place preference. In the former group (*V. simillima* and *V. analis*) the envelope is usually thick, covering the combs completely. In developed nests of these species the envelopes consist of multilayered shell-like sheets enclosing many air chambers among them. In the latter group (*V. crabro*, *V. tropica* and *V. mandarinia*), the envelope consists of only a few plate-like sheets with imperfect air chambers, and the lowest comb is always exposed.
- 4) The foods of *Vespa* consist of two well defined classes, carbohydrate and protein. The former are obtained from tree sap, honey-dew of aphids and psyllids, flower nectar, mushroom and syrup juice. The most important source for all the *Vespa* species was the tree sap exuding from apertures of living trees. Both intra- and interspecifically a distinct linear dominance order is recognized among the hornets visiting tree sap. Interspecific relationships among both queens and workers at food sources are as follows: *mandarinia* - *analis* - *crabro* - *simillima* - *tropica*.
- 5) Prey preference of *Vespa* differed characteristically with species. *V. simillima* and *V. analis* hunt a wide range of insects and spiders. *V. crabro* is regarded as a semi-specialist, preferring various kinds of cicadas, and is highly specialized behaviourally for capturing cicadas. *V. tropica* is a typical specialist, being almost exclusively dependent on the brood of polistine wasps for their protein food and the life cycle was synchronized with that of the prey wasps. *V. mandarinia* attacks in mass the colonies of other social wasps and honeybees, possessing an ability to hunt a wide variety of large insects and spiders. Group predation consists of three phases, hunting, slaughter and nest occupation.
- 6) The queen of *Vespa* hornets do not engage in cell initiation after worker emergence, though she still participate in intranidal activities for a while.
- 7) Any *Vespa* worker would perform any task within a few days after emergence without a labour schedule depending on age distinction as known in the honeybee.
- 8) In the case of *V. analis* worker oviposited a few days after the death of the queen. This 'substitution queen' was characterized by the following points; (1) acting as the primary or sole egg-layer, (2) loss of hairs on the gena and mandibular base and polished head as in the queen, (3) cessation of all extranidal activities, (4) superior dominance, (5) receiving a great deal of food from the other workers, and (6) remarkable prolongation of life span.
- 9) Total duration of brood development from egg to adult varies on the average from 30.8 days in *V. simillima* to 40.1 days in *V. mandarinia*. There is a tendency for the larger the body size in adult hornets, the longer the duration became among the five species.
- 10) The survivorship curve during the polyethic period is of a convex type in each species; remarkably low mortality during the immature stages and high mortality after the commencement of foraging activities in the adult stage.
- 11) After the emergence of sexuals, high mortality was observed throughout all developmental stages, particularly egg and 5th instar, which was probably caused by a decrease in attention given to the brood.
- 12) The general pattern of seasonal colony development in the five *Vespa* species is characterized by slow development in the early stage, followed by explosive development in the later stage and then the rapid and terminal decline after sexuals have been produced. The colonial life of *V. tropica* is about 3.5 to 4 months, while that of *V. simillima* is 7 to 7.5 months. The other three species occupy intermediate positions

between the two extremes, in the following order: *simillima* - *mandarinia* - *analisa* - *crabro* - *tropica*.

- 13) Comparing the colony size at peak, the maximum number of cells was ca. 300 in *V. tropica*, ca. 900 in *V. analisa*, ca. 4,500 in *V. mandarinia* and *V. crabro* and ca. 10,000 in *V. simillima*.
- 14) New queens emerged during the period from early September to late November in the following order: *tropica* - *crabro* - *analisa* - *simillima* - *mandarinia*. Just prior to the production of new queens, the larva: worker ratio is reduced to its lowest level, below about 2.0, in each *Vespa* species.
- 15) The minimum number of workers in a mature colony which is considered as necessary to succeed in producing new queens varies with the species. In *V. tropica* they can be produced in a colony with more than ca. 20 workers, while in *V. simillima* colonies the number of workers present needs to reach at least ca. 300 workers.
- 16) The maximum number of sexuals present per colony varied from 56 new queens and 27 males in a *V. tropica* colony to 1,692 new queens and 1,123 males in a *V. simillima* colony and is ranked as *simillima* > *mandarinia* > *crabro* > *analisa* > *tropica*. In general it is recognized that the larger the colony, the more sexuals are produced not only in the same species but also among the five species.
- 17) Mortality factors working mainly at the nest level are divided into five main causes, (1) disappearance of queen, (2) natural enemies, (3) human interference, (4) climatic factors and (5) unknown causes. The end of *Vespa* colonies occurs very frequently during the solitary period and following cooperative period when the queen continues to forage outside the nest, which is attributable to the disappearance of the queen. The heavy predation by *V. mandarinia* results in the greatest proportion of all the unsuccessful nests at mature stage in each *Vespa* species except for *V. mandarinia*. In the case of *V. mandarinia*, destruction by beekeepers plays an important role in colony mortality of mature nests.
- 18) Annual fluctuations in the number of *V. simillima* colonies surveyed in four adjacent areas covering ca. 300 ha. gave a nest density of 0.01–0.03 nests per ha. during 12 years, and the total number of nests varied from 3–10 per year.
- 19) A mechanism to explain the coexistence of the five *Vespa* species in southwestern Japan is discussed from the view point of the occupation of different ecological niches including nest site, food preference and colony cycle.

### ACKNOWLEDGEMENTS

I wish to express my sincere gratitude to Professor Shôich F. SAKAGAMI of the Institute of Low Temperature Science, Hokkaido University for his continuous guidance and encouragement throughout the present study. Cordial thanks are also due to Mr. Robin EDWARDS of Rentokil, East Grinstead, England, Dr. Michael ARCHER of College of Ripon and York St. John, England and Mr. Robert JACOBSON of East Carolina University, U.S.A., for their reading and correction of this manuscript. I also thanks Messrs. Shigeaki MIYATA, Noboru HAYASHI, Noboru YAMAMURA and Mamoru EGAWA for their kind help in the course of the present study.

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## 摘 要

### 日本産スズメバチ属 *Vespa* (Hymenoptera, Vespidae) 5種の比較生態学的研究

松 浦 誠

本論文では、日本の西南暖地の低山地から平地に阿所的に生息する5種のスズメバチ属のハチ類、すなわち、キイロスズメバチ *Vespa similis xanthoptera* CAMERON (以下キイロ)、コガタスズメバチ *Vespa analis insularis* DALLA TORRE (以下コガタ)、モンスズメバチ *Vespa crabro flavofasciata* CAMERON (以下モン)、オオスズメバチ *Vespa mandarinia japonica* RADOSZKOWSKI (以下オオ)、ヒメスズメバチ *Vespa tropica pulchra* BUYSSON (以下ヒメ) について、各種の生活史、営巣習性、採餌習性、分業、個体群の動態などを明らかにし、これらの蜂の共存の機構を考察したものである。

調査は1964年より1975年までの12年間にわたって和歌山県有田郡吉岡町とその周辺の地域で行われ、総計622巣のスズメバチ属の巣を観察の対象としている。

#### 1. 生活史

生活史の質的变化を成虫の社会関係を中心に区分するとつぎの6段階、すなわち、(1)前営巣期、(2)女王の単独営巣期、(3)女王と働きばちの共同営巣期、(4)分業期、(5)繁殖カスト産出期、(6)越冬期となる。

越冬後の女王は4月上旬より8月上旬の間に、キイロ・オオ・モン・コガタ・ヒメの順に出現する。各種とも単独創設で、受精したメス(=女王)のみが創巣し、単独営巣期に35~40房をつくり、そのうち10~15頭の幼虫を単独で育てあげる。最初の働きばちは6~7月に、キイロ・モン・コガタ・オオ・ヒメの順に羽化する。共同営巣期は2~8週間で、その長さは一般にそれぞれの種のコロニーサイズと関連があり、キイロのような大規模営巣型の種では短かく、コガタやヒメのような小規模営巣型の種では長い。働きばちの個体数の増加にともない、ヒメを除く他の4種では、女王は産卵活動に専念し、分業期の後半には、働きばちが女王をとりまくローヤルコートが出現する。オオと新女王はコロニーの働きばちの個体数が最多状態に達した時より約1ヶ月以上にわたって産出され、交尾は巣外で行なわれる。営巣活動の終息は9月上旬より11月下旬までで、ヒメ・モン・コガタ・オオ・キイロの順となっている。

#### 2. 営巣習性

営巣場所は開放空間型(コガタ)、遮蔽空間型(モン、ヒメ、オオ)、両空間型(キイロ)に区別される。キイロとモンは営巣当初は狭い遮蔽空間を嗜好する傾向があるが、働きばちの羽化後の7~8月に、より広い遮蔽空間(モン)および開放空間(キイロ)へコロニーが移住したのち新女王の産出を行なうことが多く、営巣末期の巣ではキイロ88.6%、モン53.5%が引継ぎ巣であった。

巣の構造は、女王巣の場合、外殻の形状により3型、すなわち、皿型(ヒメ、オオ)、筒型(モン、キイロ)、徳利型(コガタ)に区別される。成熟巣では、開放空間嗜好種のコガタとキイロでは、外殻は貝殻状をした多数の空気室で構成され、ただ1個の側部の出入口を残して巣盤全体を完全に被覆するが、遮蔽空間嗜好種のモン、ヒメ、オオでは、外殻は不完全な空気室をもった数枚のシートで構成され、最下段の巣盤が常に露出して出入口を兼ねる。

#### 3. 採餌習性

炭水化物源は5種ともに共通し、樹液、半翅目昆虫の甘露、花蜜、熟果、キノコ(シラタマタケ)、空腐や空びん内に残されたジュースなどで、最も重要なものは樹液とキノコである。

蛋白質源となる食物とその採餌行動には顕著な種間差がみられる。キイロとコガタは「何でも屋」で、前者は8目44種以上の昆虫やタモを狩り、そのうちの60%は双翅目の成虫で占められたが、後者は8目53種以上でそのうち双翅目成虫37.9%について膜翅目の有刺翅成虫も32.2%を占め、アシナガバチ亜科やスズメバチ亜科の種も含まれる。モンは食物の95%以上がセリ類によって占められるが、大型のトンボ、バッタなども捕える能力をもち「専門家」とみなされる。ヒメは典型的な「専門家」で、アシナガバチ亜科の各種の巣を襲って、その幼虫と蛹の体液のみを摂取す

る。オオは単独ではドウガネブイブイなどの中型のコガネムシ類を中心に、多肉で動きの鈍い昆虫やタモを狩る「専門家」であるが、同じ巣の働きばち集団が、同属他種のスズメバチ、クロスズメバチ属、ミツバチ属などの社会性ハチの巣を襲い、相手を全滅させたのも幼虫や蛹を掠奪する習性を発達させている。これが、明治以降にわが国へ導入されたセイヨウミツバチに対する集団攻撃の起源とみなされ、単独捕食期、集団殺戮期、占領掠奪期に区別して解析した。

#### 4. 分業

女王は働きばちの羽化後は、外役、ついで内役の順に引退したのち産卵に専念する。モンの女王の場合、巣づくり行動には、働きばちの出現後も約40日にわたって参加したが、この間に(1)育房の新設、(2)みずから野外で集めた巣材による外被や房壁の伸長、(3)外被をかじりとり得た巣材による房壁の伸長、(4)巣材を集めずに、働きばちが伸ばした直後の湿った房壁の再加工（薄く伸ばす）の順に停止する。

働きばちの日給と仕事に関しては、5種ともに羽化後2日目より各種の内役を行ない、3～4日目には定位飛行ののち、すぐに巣材、食物、水などの採集活動に従事し、老齢化しても、巣の内外のあらゆる仕事をこなす能力をもつ。

女王の亡失後には、数日後に働きばちの一部の卵巣が発達し、女王の代位となる個体が出現する。コガタの場合、「代位女王」は次の特性をもつ。(1)唯一の、または最優位の産卵者としてオスを産出する。(2)分業期の女王にみられるような体毛の脱落、および体表面が油じみた光沢をもつ。(3)あらゆる外役への不参加、(4)他の働きばちに対する優位行動、(5)他の働きばちからの頻繁な食物摂取、(6)寿命の著しい延長。

#### 5. 個体群の動態

働きばちの卵から羽化までの発育所要日数は種によって異なり、分業期ではキイロの30.8日からオオの40.1日までの幅があり、大型種ほどその期間が長くなる傾向がある。

働きばちの生存曲線は、5種ともに典型的な凸型を示し、卵から羽化後2～3日目までの非外役期では非常に死亡率が低い。外役活動の開始とともに死亡率が一定割合で起こり、小型種ほど成虫の寿命が短い傾向を示した。また、新女王の羽化の始まったコロニーでは、働きばちの給餌対象が幼虫から新女王成虫へと転換し、そのため幼虫の餓死や非成虫個体に対する共食いが急増して、営巣活動の崩壊を促進した。

営巣期間は種によって異なり、短期営巣型のヒメは3.5～4ヶ月に過ぎないが、長期営巣型のキイロは7～7.5ヶ月で、他の3種はキイロ・オオ・コガタ・モン・ヒメの順に両者の中間に位置する。

営巣規模は顕著な種間差があり、小規模営巣型のヒメは最多育房数で300房であるが、大規模営巣型のキイロでは10,000房に達する。オオとモンは中規模営巣型とみなされ最多育房数で4,500房となるが、コガタは1,000房以下で小規模営巣型とみなされる。

新女王の羽化期も種によって異なり、ヒメ・モン・コガタ・キイロ・オオの順に、9月上旬より11月下旬までの幅がある。新女王の産出にさきがけ、幼虫・働きばちの割合(L/W比)は各種とも全営巣期を通じて最低値に下降し、その値は2.0前後となっている。

新女王の産出のために必要な働きばちの個体数は種によって著しく異なり、ヒメでは約20頭以上であるが、キイロでは少なくとも300頭以上とみなされ、他種は両者の間に位置する。

コロニーあたりの新女王とオスの産出数は、一般にコロニーサイズが大きくなるほどその数も多くなり、その最大値はキイロで新女王1,692頭、オス1,123頭、最少値はヒメで新女王56頭、オス27頭であり、5種ではキイロ>オオ>モン>コガタ>ヒメの順になっている。

廃巣要因は、女王の亡失、天敵（オオスズメバチ、ハチタマ、スズメバチネジレバネなど）、人の干渉、気象、不明などで、5種ともに単独営巣期から共同営巣期の段階において、女王の亡失による廃巣が最も多くなっている。

巣の年次変動に関しては、キイロの場合、300 haにおける12年間の成熟巣の数をみると3～10巣/年と低密度の安定型を示した。巣あたりの新女王の生産数の多さに比べ、巣の密度が非常に低いので、本種は強力な密度の自己調節能力をもつとみなされるが、他の4種もその可能性をもつ。

以上の結果から、これら5種のスズメバチは、営巣習性、採餌習性、新女王の生産期などの生態的地位をそれぞれ異にすることによって相互の競争的関係を少なくして、同所的に生息を可能にしているものと推論した。