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Author(s)	MATSUURA, Makoto; SAKAGAMI, Shôichi F.
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A Bionomic Sketch of the Giant Hornet, *Vespa mandarinia*, a Serious Pest for Japanese Apiculture

By

Makoto Matsuura and Shôichi F. Sakagami

Oki, Kibi, Wakayama and Zoological Institute, Hokkaido University, Sapporo

(*With 12 Text-figures and 5 Tables*)

Many Japanese beekeepers who consult standard books on apiculture published in Europe or North America must feel a strong discontent after reading through the chapter dealing with bee enemies. They may find there little or no information on the hornets or the genus *Vespa*, which have extirpated annually thousands of bee hives in Japan. The poor information depends on the uneven northward expansion of this predominantly subtropical genus. Most parts of Central and North Europe are inhabited by a single species, *V. crabro*, which is relatively innoxious to the European honeybee, *Apis mellifera*. The genus has been confined to the Old World before *V. crabro* was accidentally introduced into Eastern North America and established there.

On the other hand, there exist at least six species of *Vespa* in Japan and two of them, *V. mandarinia* and *V. mongolica*, cause serious damage to bee hives. Especially, the former, the giant hornet, is famous to beekeepers for its catastrophic attacks. Many observations have been reported on its habits by Japanese beekeepers. Okada (1956, 1961 a, b, c) described some aspects of its bionomics. However, previous descriptions are mostly fragmentary or superficial, not precisely dealing with the bionomic or ethologic characters of this species, which are quite different from those of other congeneric species. The purpose of the present paper, the summary of which was presented in Sakagami and Matsuura (1972), is to give a preliminary outline of its bionomics in comparison with other species, with special reference to attacks on bee hives, leaving further studies on particular aspects elsewhere.

Most observations were made by M.M., while S.F.S. mainly participated in the bibliographical survey and preparation of the manuscript. We wish to express here our sincere appreciations to many beekeepers, especially Messers Y. Asai, K. Fujii, K. Ishii, Y. Hanada etc., who gave us valuable information on the attacks of *V. mandarinia* on bee hives, and

to Prof. Charles D. Michener, Department of Entomology, University of Kansas, Lawrence, who read through the manuscript.

1. Taxonomic notes on the Japanese hornets

To facilitate further work a brief taxonomic comment on the hornet species inhabiting Japan is given, mainly based upon Vecht (1957, '59). The following forms are so far recorded from Japan:

V. analis insularis Dalla Torre 1894.

V. bicolor Fabricius 1787. Recorded by Du Buysson (Vecht 1957), but in all probability it does not occur in Japan.

V. crabro flavofasciata Cameron 1903.

V. dybowskii André 1884.

V. mandarinia latilineata Cameron 1903.

V. mongolica André 1884. Since Sonan (1935) placed *V. mongolica* as synonymous to *V. simillima*, *V. xanthoptera* Cameron 1903 has long been used in Japan for this species. Here we adopt *mongolica* following Vecht, but we are not sure of the valid name of this species.

V. simillima Smith 1868.

V. tropica pulchra Du Buysson 1905.

V. walkeri Du Buysson 1905. This taxon is unknown to us. Recently Vecht (1959) recorded it from Central Japan, but we have so far never encountered the form coinciding with the original description (Du Buysson, 1905, p. 519).

Of these forms, *V. simillima* is confined to Hokkaido, being considered as the vicariant of *V. mongolica*, but further critical comparison is required as to their taxonomic rank, either specific or subspecific. Among other forms, only *V.*

Table 1. Main climatic conditions in Kibi (1962~'70)

Month	Temperature (C°)			Rainfall (mm)
	Mean Maximum	Mean	Mean Minimum	
Jan	8.7	4.5	0.4	76.7
Feb	9.5	5.0	0.6	59.3
Mar	13.0	8.1	3.1	126.8
Apr	19.1	14.4	9.7	168.2
May	23.7	18.7	13.6	176.2
Jun	25.9	21.8	17.6	264.0
Jul	30.3	26.2	22.2	231.3
Aug	31.6	27.2	22.8	164.1
Sep	28.0	23.5	19.1	195.2
Oct	21.9	17.2	12.5	101.2
Nov	17.1	12.3	7.4	112.2
Dec	11.7	7.2	2.8	58.4
Mean	20.0	15.5	11.0	Total 1,733.8
Extremes	35.7		−4.7	

mandarinia and *V. crabro* reach northward to Hokkaido while others are confined to the southern islands. *V. dybowskii* is peculiar in some habits (Sakagami and Fukushima 1957a) but is sporadically distributed and rare. Therefore, the forms mainly referred to below are *V. mandarinia, mongolica, crabro, analis* and *tropica.* Most observations were made in and near Kibi, Wakayama Prefecture. Main climatic conditions in the locality are given in Table 1.

V. mandarinia is easily distinguished from other species by its huge size, deeply incised clypeus and enormously developed genae, which give it a strange

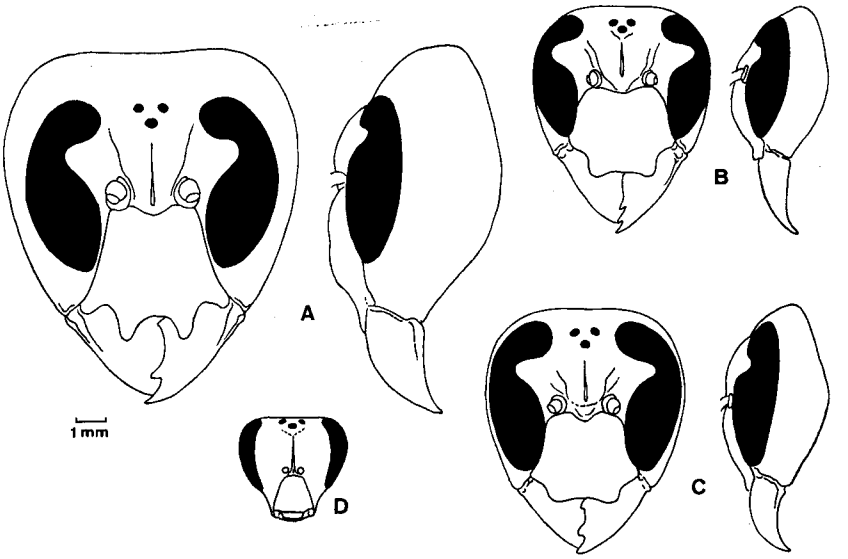

Fig. 1. Head of workers of three Japanese species of *Vespa* (Frontal and profile views). A. *V. mandarinia,* B. *V. mongolica,* C. *V. crabro,* D. *Apis mellifera* for comparison.

Table 2. Some measurements of relative size of five Japanese *Vespa* species (mean of five workers for each species)

Species	Body weight relative to *V. crabro*[1]	Head width (6 units=1 mm)	Mandibular length (6 units=1 mm)	Head width / outer orbital distance	Genal width / eye width in profile
mandarinia	1.60	57.4	28.2	1.15	2.44
tropica	1.18	47.2	21.7	1.02	1.26
analis	1.15	47.0	21.6	1.02	1.38
crabro	1.00	46.9	21.4	1.03	1.57
mongolica	0.92	39.6	20.4	1.00	1.48

1) Based upon alcoholed specimens. Fresh weight of *V. mandarinia*: Queens 2.0~3.0 gr, workers and males 1.0~1.5 gr (Okada 1961 b)

physiognomy (Fig. 1, cf. also Table 2). On the basis of the general trend in vespine morphology, these features can be assumed to be specialized or apomorphic conditions. Some relative measurements of five species are given in Table 2.

V. mandarinia is widely distributed in East and Southeast Asia southward to Peninsular Thailand but does not invade the true humid tropics (Vecht 1959). Several local forms are named as follows: *m. mandarinia* Smith (China), *m. latilineata* Cameron (Japan), *m. nobilis* Sonan (Formosa), *m. magnifica* Smith (China, Indochina, Thailand, Burma, N. India), *m. soror* Du Buysson (Laos, China).

2. Nesting habit

2.1. *Nest sites*: All observed species prefer mountain outskirts and hill sides, being relatively scarce in plains. Mainly based upon the data obtained in and near Kibi, Matsuura (1971a) distinguished three nest sites used by these species: Free-aerial (F), above ground but in concealed cavities (C) and subterranean cavities (S), and gave the specific differences as follows: *analis* (exclusively F), *mongolica* (eurytopic, but $F > C \geq S$), *dybowskii* (mainly C), *tropica* and *crabro* ($C \fallingdotseq S$), *mandarinia* (exclusively S). The nest site preference of *V. mandarinia* is fairly fixed. Some previous records of above-ground nidification must be erroneous. Among 31 nests examined, 25 were found in subterranean cavities formed around rotten pine roots or those made by small rodents, snakes, etc., and six in subterranean tree hollows, with the depth to the top of the nest 6 to 60 cm. The preexisting burrow connecting cavity and ground surface is used as the entrance canal (Fig. 3b), with the length varying from 2 to 60 cm and the direction either horizontal (17 cases), inclined (7) or vertical (7).

The founding queens prefer rather narrow cavities. The nest primordium is attached to the roots 2 ~10 cm wide or to the surface of pebbles on the roof of the cavities. After the emergence of workers, nest cavities are extended as soil adjacent to the nest envelope is constantly removed and thrown away from nests. Each worker removes soil particles and prepares a small ball with mandibles and fore-legs. Keeping the ball in the mouth, she leaves the nest on foot and drops the ball not far from the entrance. At the peak of nest expansion a tongue like platform of removed soil appears at the entrance, which attained in a highly developed case 2 m in length, 50 cm in width and 15 cm in the maximum depth. This habit is sharply contrasting to other species, which throw away removed soil on the wing.

2.2. *Nest structure*: The nest is characterized by a poor development of the envelope (Fig. 2A, Fig. 3a). In incipient nests the envelope remains in an inverted bowl-shape (Fig. 2E), never extending below to completely cover the incipient comb as in *V. crabro* and *V. mongolica* (Fig. 2F, cf. Matsuura 1971a). In developed nests the envelope consists of one to three plate-like sheets of rough and imperfect texture, being quite different from the elaborated envelopes of *V. crabro* and

especially of *V. mongolica,* which consist of multilayered shell-like sheets involving many aerial chambers between them. In *V. crabro* the envelope covers the lower combs (Fig. 2C). In *V. mongolica* even subterranean nests are completely enveloped and communicate with nest cavities by means of a single neatly made hole (Fig. 2D). In *V. mandarinia* the cover is incomplete and the lowest comb is always exposed within the nest cavity.

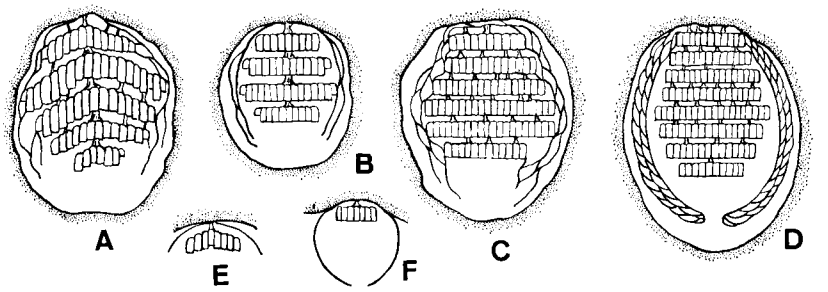

Fig. 2. Patterns of subterranean nests of four Japanese species of *Vespa.* A. *V. mandarinia,* B. *V. tropica,* C. *V. crabro,* D. *V. mongolica,* E. *V. mandarinia,* incipient nest, F. *V. crabro* and *V. mongolica,* incipient nest.

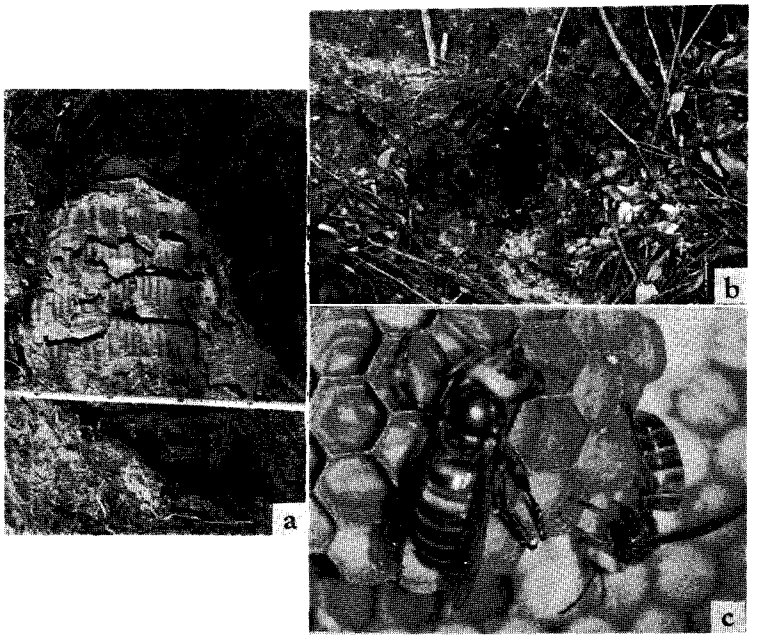

Fig. 3. Nest of *V. mandarinia.* a. Nest at late nesting period, b. Nest entrance with guards, c. Queen (left) and a worker on comb.

The dorsal surface of each comb is conical, higher at the center and new cells are added in lower marginal positions. The surface is rough and the bottom of each cell is easily recognized, contrasting to the horizontal combs with flat and even dorsal surfaces in other species, especially *V. mongolica* (Fig. 2). In other species a new comb starts always from a single central primordium, which is gradually expanded concentrically. In *V. mandarinia* the synchronous building of a few primordia and their later fusion to form a single comb is not rare.

Each comb is connected to others by one main pillar (0.8 ~2.0 cm long) and 2 ~50 auxillary pillars, and expands concentrically if there are no obstacles, but results in fairly irregular shapes when the development is hindered by rocks, roots, etc. In nests taken in November, after the cease of expansion, the number of combs per nest is 4 ~7, mostly 5 ~6. The top comb is abandoned after summer and is rotted by molds, whereas *V. crabro* and especially *V. mongolica* strengthen the top comb by filling brood cells with exogenous materials and utilize it as a strong support for the lower combs. The largest comb lies at or below the middle of the nest. Two largest combs so far measured were: 1) 49.5 cm×45.5 cm with 1,192 cells (circular) and 2) 61.0 cm×48.0 cm with 1,191 cells (elliptical, embracing a pine root).

2.3. *Brood cells*: The average size of brood cells is given in Table 3. Cells for workers and sexuals are different in size, a trait common to all species of the Subfamily Vespinae which has the highest caste differentiation linked with monogyny in social wasps (Fig. 3c). The numbers of cells in two nests, being extreme in size among nine examined after the end of nest activity, are given in Table 4. The mean comb and cell numbers of these nine nests are: 5.9 combs, 553.6 uncocooned cells (incomplete 14.0, half-built 59.3, complete 480.3) and 2,250.4 cocooned cells. Comparing the size with other species, the number of cells produced is ranked as *mongolica*≫*mandarinia*≥*crabro*≥*simillima*>*analis*≫*tropica*. *V. mandarinia* occupies the second rank but is far inferior to *V. mongolica*.

In the top comb built by the founding queens, cells are used 2 ~3 times; single usage and use more than three times are so far unknown. In combs built by workers, cells of the upper combs are used 2 ~3 times and of lower ones 1 ~2 times.

Table 3. Size of brood cells (mm)

	Diameter			Depth		
	minimum	mean	maximum	minimum	mean	maximum
Worker cells built by						
queen	9.1	10.8	12.0	26.7	32.7	35.0
workers	11.2	13.1	14.2	31.6	34.3	36.6
Queen cells	14.0	14.8	15.5	39.2	42.1	43.8
Male cells	14.0	14.5	15.3	39.3	39.8	40.3

Table 4. Number of cells in two nests taken after cessation of adult activities (* unsorted for decaying)

Comb No. (from top)	Diameter of comb (cm) long	short	Number of pillars	Uncocooned cells incomplete	half-built	complete	Cocooned cells (Number of uses) 1	2	3	Total
The smallest nest (4 December '65, Yuasa, Wakayama Pref.)										
1	17.0	16.0	?	0	0	0	——	157*	——	157
2	32.5	29.0	5-	0	0	16	288	113	0	417
3	32.0	19.5	9	1	24	97	189	53	0	364
4	25.0	18.0	10	0	9	76	142	0	0	227
5	19.5	15.5	5	1	4	45	87	0	0	137
6	7.0	5.5	1	0	10	14	0	0	0	24
Total				**2**	**47**	**97**	——**1,029**		——	**1,326**
The largest nest (21 November '64, Kibi, Wakayama Pref.)										
1	39.0	30.0	?	0	0	9	272	593	0	874
2	49.0	43.0	36	1	4	153	697	400	0	1.255
3	49.5	45.5	38	5	11	196	642	338	0	1,192
4	45.5	41.5	31	13	53	183	542	57	0	848
5	32.0	30.0	20	6	30	209	182	0	0	427
6	11.5	11.0	1	1	3	61	0	0	0	65
Total				**26**	**101**	**811**	**2,355**	**1,388**	**0**	**4,661**

Table 5. Number of cells and age structure in a large nest taken at late active period (15 October '69, Uchida-machi, Wakayama Pref.). Number of adults: Queen 1, workers 460, males 85.

Comb No. (from top)	Diameter of comb (cm) long	short	Number of pillars	Number of immatures: eggs	larvae (instars separately) I	II	III	IV	V	pupae queen	worker	male	Number of cells: empty	total
1	42.0	34.0	40	10	7	1	1	0	34	14	25	65	924	1,081
2	61.0	48.0	48	142	22	7	19	23	197	92	149	186	355	1,191
3a	42.5	16.0	9	73	3	3	23	9	106	88	0	121	25	447
3b	37.5	28.0	14	8	3	16	22	37	115	122	0	154	9	486
4a	31.5	19.5	6	48	36	40	41	40	84	8	0	0	10	307
4b	17.0	11.5	1	4	8	15	14	7	25	3	0	0	6	81
4c	15.5	11.0	2	5	6	8	3	10	24	6	0	6	9	77
5	4.5	4.5	1	13	0	0	0	0	0	0	0	0	1	14
Total				**303**	**85**	**90**	**123**	**126**	**585**	**333**	**174**	**532**	**1,339**	**3,684**
					———		1,009	———		——	1,039	——		(3,690)

Total number of cells (3,684) is not equal to the sum of immatures and empty cells (3,690), because some cells received more than one egg

But even in the top comb some peripheral incomplete cells appear to be unused, judging from the absence of cocoon residues. In the lower combs, cells producing workers again receive worker eggs, but after September male eggs (These cells are not included in male cells given in Table 3). Queen and male cells after the first usage receive male eggs.

The rearing of sexuals starts after September. Table 5 shows the age structure of the largest nest so far taken during the active period. The nest was at the stage of male emergence. New queens still had not emerged, remaining in cocoons.

2.4. *Comparative notes on nest structure*: The descriptions given above suggest some bionomic characters specific to *V. mandarinia*. Although the shift from subterranean to epigaeic nidification is regarded as a rule in aculeate Hymenoptera, the secondary return to the subterranean life is known in some winged social groups, stingless bees and wasps. In the latter, the subterranean life appears only in Vespinae (*Vespula* and *Vespa*) and some Neotropical polybine genera (for instance, some species of *Stelopolybia*, Sakagami and Zucchi, unpub.) The exclusive subterranean nidification of *V. mandarinia* is hence regarded as a specialized habit.

On the other hand, some peculiarities of nest structure enumerated above appear to be primitive: 1) Conical dorsal surface of combs. 2) Uneven texture of comb surface. 3) Envelope consisting of only a few plate-like sheets with imperfect aerial chambers. 4) Incomplete coverture of nest by envelope. 5) Occasional formation of a comb by fusion of several primordia. 6) Later abandonment of top comb.

However, some of these characters, especially 1 and 3～5, could be regarded as adaptations to exclusive subterranean nidification, partly in connection with the preference by founding queens for relatively narrow cavities, which are later expanded according to nest development. Comparing two subgenera of *Vespula*, *Vespula* s. str. and *Dolichovespula*, Weyrauch (1935–6; *Vespula* and *Vespa* in the current usage are in his system respectively *Vespa* and *Macrovespa*) asserted that *Vespula* as a group is more advanced than *Dolichovespula*, citing, among various characters, the following nest structures:

Characters	*Dolichovespula*	*Vespula*
Nest site	Often free aerial, rarely subterranean	Always concealed, frequently subterranean
Colony size, comb and cell numbers	Small	Large
Number of envelope sheets	11～12	3～4
Comb shape	Concave, with a poor space economy	Horizontal, with a higher space economy

Certainly further critical studies are required to determine the relative antiquity of various nesting habits, both in Weyrauch's case and of ours. But considering other characters specific to *V. mandarinia* described in the present paper together,

it is plausible that some superficially primitive characters in nest structures are the outcome of its adaptation to subterranean nidification. In stingless bees, too, irregularly clustered nests of some groups are inferred as secondary derivation from combed nests due to spatial limitation (Michener 1961).

3. Annual cycle and related habits

The annual cycle of *V. mandarinia* consists of the following six periods: 1. Pre-nesting, 2. Solitary, 3. Cooperative, 4. Polyethic, 5. Dissolution, 6. Hibernating, as presented subsequently in this section. The sequence does not essentially differ from that in other temperate eusocial insects with annual colonies: *Vespa*, *Vespula* (s. lat.), *Bombus* and, with some deviations, *Polistes* and eusocial halictine bees.

3.1. *Pre-nesting period*: Three types of females enter hibernation, inseminated queens, uninseminated queens and stylopatized workers. In and near Kibi, they leave hibernacula in early to middle April. The days of the first encounter are: April 12 (1964), 8 ('66), 22 ('67), 6 ('68) and 11 ('69), and the interspecific order of spring appearance is, *mongolica*>*mandarinia*>*crabro*>*analis*≫*tropica* (Matsuura 1971b). Among these species *V. mongolica* occasionally visits flowers of *Camelia japonica* var. *spontanea*, but other species seldom frequent flowers. The most important food source of post-hibernating females is the sap of *Quercus* trees, which are particularly preferred by *V. mandarinia*, with the peak of visits from late April to early May.

It was already reported that there is a distinct interspecific dominance order among the species visiting tree sap (Sakagami and Fukushima 1957a, Matsuura 1969). *V. mandarinia* invariably occupies the first rank, monopolizes favorable sap sources, and expels other hornet species, beetles, butterflies, flies, etc. This dominance is maintained to workers. For instance, queens of *V. tropica* leave hibernacula far later than other species so that they visit tree sap synchronously with workers of *V. mandarinia*. In spite of their much larger body size than *V. mandarinia* workers, *V. tropica* queens are expelled by a single individual of the latter.

Moreover, there is a distinct intraspecific dominance order among the queens of *V. mandarinia* visiting a common sap source (Matsuura 1969). When the top ranked queen is taking sap, the other queens wait their turns, forming a circle about 10 cm in diameter around the top ranked one. After the departure of the latter, other queens successively take sap according to their rank order; consequently the lower ranked ones barely feed by night.

3.2. *Solitary to polyethic period*: Besides feeding on tree sap, inseminated queens start nest site exploration in late April. Uninseminated queens do not perform such flights. Their ovaries begin to develop but soon degenerate.

Without founding nests they continue to visit tree sap, after May only in the daytime, and disappear in early July (Matsuura 1969).

The number of workers reared by a solitary queen is about 40. Cells produced by queens are smaller (Table 3) and workers emerging from them are the smallest. Their extranidal activities start in early July. No direct observations of intranidal activities in subsequent periods have yet been made. The following description was based upon observations on nest contents and extranidal activities.

After the emergence of first workers, queens still participate in extranidal activities for a while (Cooperative period). But from about mid July they cease to leave nests in parallel with the increase in numbers of workers (Polyethic period). In early August, well developed nests contain three combs, about 500 cells and 100 workers. After late August the cell size increases and male eggs are laid. After mid September, worker eggs are produced never more and larvae of sexuals are reared. Survival of founding queens was confirmed in all nests examined before 19 October, but not after 26 (1968) ~31 (1967) October. In *V. crabro* and *V. analis* (Matsuura, unpub.), colonies enter a disorganized state with the death of founding queens. Workers fight one another and nest development ceases, though foraging activity continues. After 3 ~4 days, the colonies recover the lost harmony in parallel with the appearance of laying workers. A similar situation is expected in *V. mandarinia* but there are still no direct observations.

3.3. *Dissolution and hibernating periods*: Males and new queens begin to emerge in mid September and mid October, respectively. Both remain for a certain period within nests, during which they receive food from workers and larvae. Their body color gradually intensifies and body weight increases in queens (from 2.9 to 3.5 gr., Matsuura 1966). The departure from nests takes place after early October in males and early November in queens, both on fine days. Workers are indifferent to their departures. Departing sexuals do not make orientation flight and never more returns to nests. In other hornet species copulation occurs away from nests and males do not visit nests. Only in *V. mandarinia* do males visit nests and await departing queens at nest entrance to mate with them. The departure of new queens takes place mainly in forenoon. At this time many males (up to 69, 13 Nov. '66) swarm in the air, occasionally resting on twigs and leaves nearby. The male seizes the queen in the air. Then both fall down on the ground where the copula is performed, lasting 8 ~45 sec. (9 cases), far shorter than in *V. mongolica* (5 ~10 min.). After mating the male returns to the nest for a second chance and the queen leaves straightly, probably searching for a hibernaculum. It is remarkable that many queens shake off males and leave nests without mating. This trait must be responsable for the presence of numerous uninseminated queens in spring (63.5 ~67.5% of hibernating queens, Matsuura 1969).

At the time of emergence of the sexuals, foraging activity of workers changes from animal food to carbohydrates (tree sap, fruits, etc.). No more protein food

pours into nests near the dissolution of colonies. Nest activities cease in late November. The last emerged sexuals cannot obtain sufficient food. They leave nests without maturing and all die of hunger.

All hibernating queens so far discovered were found in subterranean hibernacula (Matsuura 1966), which are spherical chambers made in moderately moist soil near the ground surface. The queen passes the winter hanging from the top of the chamber. The single exception was a queen found within an abandoned nest of *V. crabro* made 30 cm above the ground. These habits are common to other hornet species and differ from *Vespula* and *Polistes* wasps in their predominantly solitary hibernation (rarely two) and preparation of hibernating chambers instead of mere utilization of pre-existing cavities.

3.4. *Extranidal food regurgitation*: The annual cycle of *V. mandarinia* sketched above does not differ greatly from that of other hornet species, except for copulation at nest entrances. Another habit peculiar to this species, the frequent extranidal food regurgitation, is referred to here.

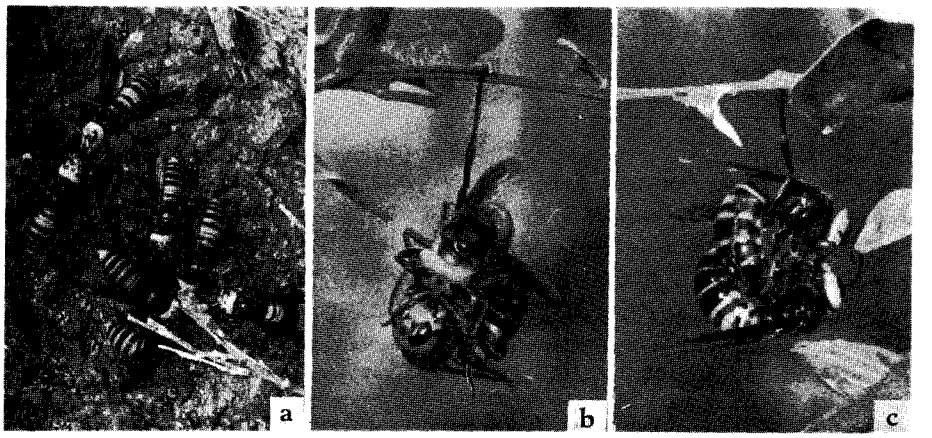

Fig. 4. Extranidal food regurgitation in *V. mandarinia*. a. a group of workers belonging to the same nest at a *Quercus* tree sap source, with two workers at trophallaxis, b and c. Trophallaxis between two starved workers, hanging down from a tree twig.

The food regurgitation between workers was confirmed within nests of *V. crabro* and *V. analis* (Matsuura, unpub.), but not outside of nests in any species, with a single exception of two workers of *V. crabro* visiting a tree sap source. On the other hand, this behavior outside of nests is very common in *V. mandarinia* (cf. also Okada 1961 a). The situation is most frequently encountered among nest mate workers visiting the same tree sap source (Fig. 4 a). In this 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 (Fig. 4 b, c), they alternately beg and receive food. The embrace lasts from several to tens of minutes and they do not easily separate even if disturbed with sticks, etc. Such reciprocal trophallaxis is occasionally seen when this species attacks bee hives or nests of other social wasps, especially near the victim's nest during prolonged atttacks, but so far is not confirmed within or near 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 relate to its preference for such concentrated food sources.

4. Attacks by hornets on bee hives

The attacks on bee hives by *V. mandarinia* are quite different from those by other observed species. Before referring to its peculiarities, some general accounts on visits and attacks by hornet species other than *V. mandarinia* to apiaries are described.

4.1. *Visits by Japanese hornet species on apiaries*: The relative frequency of visits to apiaries by various *Vespa* species and their relative abundance estimated by other measures in and near Kibi are ordered approximately as follows, partly including *Vespula* (*Paravespula*) *lewisii*, the commonest yellow-jacket in Japan:

Visits to apiaries: *mandarinia*$\gg$*mongolica*$\gg$*crabro*$>$*analis*$>$*lewisii*$>$*tropica*.
Visits to tree sap sources: *mandarinia*$\gg$*crabro*$\geq$*analis*$\geq$*tropica*$>$*mongolica*.
General extranidal activities: *lewisii*$>$*mandarinia*$>$*tropica*$>$*analis*$\geq$*crabro*$\geq$*mongolica*.
Visits to houses: *tropica*$\gg$*crabro*$\fallingdotseq$*mandarinia*$\fallingdotseq$*mongolica*$\fallingdotseq$*analis*.
Nest discovery: *mongolica*$\gg$*analis*$>$*lewisii*$>$*crabro*$>$*mandarinia*$>$*tropica*
Discovery of hibernating females: *tropica*$>$*analis*$>$*crabro*$>$*mongolica*$>$*mandarinia*$>$*lewisii*.

The marked discrepancies among different crude estimates show as a whole how difficult is to accurately estimate the relative abundance of species in a group such as *Vespa*, with a wide flight radius and relatively low density. For instance, as to nest discovery, the highest rank occupied by *V. mongolica* is well explained by its huge nest size and preference for aerial nidification. *V. analis* seems relatively rare but its exclusively aerial nests must easily be discovered. Among other species, the lower rank of *V. mandarinia* may reflect its exclusively subterranean nidification while that of *V. tropica* in part the real rarity. Nevertheless, the latter is frequently encountered near houses, because of its remarkable stenophagy, taking most of its food from *Polistes* wasp nests (Sakagami and Fuku-

shima 1957b). It is interesting that *V. mongolica,* indubitably one of the commonest species, is the lowest-ranked in visits to tree sap and general extranidal activities. Apparently this species does not visit tree sap so frequently as other species. But it is plausible that this swift and agile species has a capacity to forage from various food sources scattering out of our reach. Summarizing, discrepancies given above could be an outcome of interspecific differentiation of ecological niches, which is, for the time being, difficult to express quantitatively. In general, however, *V. analis* and *V. tropica* are regarded as less common than other species, even though the latter is, for unknown reasons, frequently discovered in winter.

Among the species visiting apiaries, *Vl. lewisii* principally seeks stored honey and steals from weak hives, but occasionally carries back the meat ball prepared from mesosomas of worker honeybees killed by *V. mandarinia. V. tropica* occasionally visits apiaries and is captured by hornet traps (cf. **7. 2.**) but so far no attack by this species, the mildest among the Japanese hornets, has been confirmed (The species seems harmful to bees in India. cf. **4. 3.**). *V. crabro* and *V. analis* actually hunt worker honeybees at apiaries but their visits are scarce and not constant. Consequently the majority of attacks on bee hives by hornets are made by *V. mandarinia* and *V. mongolica.*

The relative abundance of these two species varies according to year and locality. Generally *V. mongolica* is more harmful in Northern Japan and *V. mandarinia* in Southern Japan, judging from correspondence cited in bee journals (usually reported as large and small hornets respectively). Some samples trapped by beekeepers and sent to us for identification are given below:

			Number of hornets trapped					
Locality	Year	Collector	*mandarinia*	*mongolica*	*analis*	*crabro*	*tropica*	Total
N. Japan								
Tazawa, Akita Pref.	1967	K. Ishii	136	905				1,041
S. Japan								
Kibi, Wakayama Pref. (incl. those flew away)	1968	M. Matsuura	695	28	7	1	3	734
Yamaguchi, Yamaguchi Pref.	1964	K. Fujii	695	176		14	9	894

4.2. *Honeybee hunting by* Vespa mongolica: Attacks and hunts of honeybees by *V. mongolica, V. crabro* and *V. analis* are essentially of the same type, so that here the description is given for the first species alone.

V. mongolica is the smallest hornet in Japan (Fig. 1 B, Table 2), but builds the largest nests, inhabited by more than 1,000 workers. Probably because of its relatively euryphagous nature, visits to apiaries do not always coincide with the presence of its nests nearby. In one case (Kibi), three hives were located in a

farm. There were three large nests of *V. mongolica* within 100 m of the hives and other 5~7 nests within 1 km. From observations with marked individuals, however, visits to the hives were only 2~3 workers per day from July to November, capturing individually 0~3 bees per hour.

Visits by *V. mongolica* to apiaries continue from May to November, occasionally more abundant in mid September but not forming a definite peak as in *V. mandarinia* (cf. **5. 1.**). Without concentrating on particular hives, *mongolica* workers wait in the air or near the hive. Occasionally they approach the hive entrances but do not wait there so persistently as *V. mandarinia*, readily escaping the counter-attack by a bee worker. Because of their small size, *mongolica* workers, particularly dwarf ones in early season, are less apt to catch bees with the mandibles as does *V. mandarinia*. This defect is compensated by their agile flight activity. After catching a bee, the worker invariably flies to a tree branch nearby and hangs, head down, by one or two hind legs. Using mandibles and fore legs, she rapidly isolates the victim's mesosoma from other body parts, transforms it to a meat ball by chewing and brings it back to the nest.

Thus the attack by *V. mongolica* is by individual hunting, giving no acute and catastrophic result as *V. mandarinia* does. But, because of its lasting visits and agile behavior, it can cause chronic damage to the whole apairy. *V. mongolica* rarely frequents the apiaries visited by *V. mandarinia*. Even though visiting, they are chased away or attacked by *V. mandarinia*, which attempts to catch *V. mongolica* and if successful, brings it back to the nest after preparing a meat ball in a manner similar to that performed by *V. mongolica* described above. Recently visits by *V. mandarinia* to apiaries seem to have decreased in some areas, either because of frequent trapping or for unknown causes, probably changes of the environment. In such circumstance, visits by *V. mongolica* might increase in compensation. Fujii (1967), for instance, recorded the trap catch in 1966 in Yamaguchi as follows: small (=*mongolica*) 1,633, middle (various species including small workers of *mandarinia*) 29, large (=*mandarinia*) 25. The ratio between the two species is inverse from the prior result given at the end of **4. 1.** Saitô (1964) reported in Nagano Pref. visits to an apiary by 500 workers of *V. mongolica* per day and catch of at least ten bees per hornet. He estimated a loss of 5,000 bees per day or 150,000 per month (equivalent to five hives). Although this probably overestimates the damage, the potential destructive power of *V. mongolica*, so far concealed by *V. mandarinia*, must be pointed out, in connection with the difficulty of trapping this species because of its small size and agility.

4.3. *Previous records on damage by hornets to apiaries outside of Japan*: In this section, we attempt to compile previous information on hornet damage to apiaries outside of Japan. The bibliographical survey is by no mean complete. Numerous papers are scattering in bee journals difficult of access. Many papers were cited from the abstracts in "Bee. World" and "Apicultural abstracts". Unless particularly mentioned, scientific names follow those used in original papers.

affinis, Sonan (1927, cited as *V. formosana*), Formosa. Occasionally attacking bee hives and robbing larvae and pupae.

analis, Vecht (1957), Indonesia. Immediate excitement and attack when a comb of *Apis javana* was offered to a caged hornet colony.

basalis, Smith (1960), Punjab. Attacks on hives.

crabro, Borchert (1949), Germany. A nuisance when abundant. Hunting bees on flowers, from swarms or at hive entrances, and occasionally entering hives. Bees have difficulty killing it. Catching bees in the air, licking the honey in crop, then separating the mesosoma and bringing back it to nest. Alber (1953), S. Italy. Damage to bee colonies.

cincta, Muttoo, after Smith (1960), Madras. Exterminating hives by persistent attacks. Controls: narrowing hive entrances, poisoning hornet nests. Subbiah and Mahadevan (1957), India, Plains. Hunting at hive entrances in June~December at the period of weak bee activities, resulting in absconding or extermination. Controls: Nest poisoning by parathion, removal of entrance platform. Gravely (1915, after Vecht 1957), India. Frequently hunting honeybees. Toumanoff (1939), Indochina. Damage to bees in plains.

ducalis, Toumanoff (1939), Indochina. Damage to bees in mountains.

magnifica, Smith (1960), India, Hills. The worst enemy of bees. Toumanoff (1939), Indochina. Damage to bees in mountains.

mandarinia nobilis, Matsuura (unpub.), Formosa. The worst enemy for apiculture. Many beekeepers transfer hives (*Apis mellifera*) in summer from mountains to plains to avoid the damage.

orientalis, Wafa (1956). The worst season mid August to mid September (=late summer) after cessation of brood rearing in hives. Winter recovery difficult and often the whole apiary exterminated. Alber (1963), S. Italy. Serious damage. Bait poisoning by fish meat and sodium arsenate. Nosenko (1963), Uzbekstan, Tanscaucasia. Serious damage. Adsay (1950, cited as *V.* sp., probably *orientalis*), Turkey. Serious damage. One hornet attacking 73 times per day, carrying back 57 bees. Control: Keeping native chickens reared with hornets at apiaries. Rivnay and Bitinsky-Salz (1949), Israel. Occasionally 30% of stock exterminated. Controls: Nest poisoning and bait poisoning. Ishay et al. (1967), Israel, referred to below.

tropica var. *haematodes*, Subbiah and Mahadevan (1957), India, Hills. Hunting bees as in *cincta*.

velutina, Toumanoff (1939 cited as *auraria*), Indochina. Damage to bees in mountains. Vecht (1957), Indonesia. Probably hunting *Apis javana*.

Vespa sp. Schneider and Djalal (1970), Afghanistan. Serious to *Apis cerana* in all seasons, especially after September, with necessity of employees to kill hornets. Kloft and Schneider (1970), Afghanistan. cf. **6.2**.

From these scattered records, it is clear that various species of *Vespa* attack bee hives throughout warm-temperate to tropical Eurasia. Unfortunately most records do not describe the hunting behavior in detail. The unique precise description which we could consult was that by Ishay *et al.* (1967) on *V. orientalis*, indubitably one of the species most destructive to apiculture.

According to them, the hornets approach to bees at the hive entrance or near the apiary, "creep up on the bees. Avoiding sharp or sudden movements, grabbing a bee with her fore legs, she soars rapidly and while in flight she stings the prey to paralyse it".

Occasionally she brings the entire bee back to the nest, but usually goes to a 3~6 m high tree branch, hangs, head down, with one or two hind legs, rolls the prey between mandibles by using fore legs, throws away head and abdomen, and brings back the muscular thorax, after transforming to a chewed meat ball. Occasionally she takes the honey from the prey's crop." Further, as to the attack on the Italian bee (*Apis mellifera ligustica*), they write: "In most cases, the hornet will approach to within 1.5 cm of one of the bees standing at the entrance of the bee hive. It will then entice the bee to chase after it by executing sharp movements of retreat. The bee leaves its nest mates and follows the retreating hornet, gradually closing gap between them..... When the two have moved some 2~4 cm from the rest of the bees and are about 3~5 cm apart, the hornet pounces on the bee, grabs it with its legs and soars straight up to a nearby branch, where it commences to chew up its prey".

The behavior cited above, especially the first part, resembles in general that of *V. mongolica*. But, there are some differences which might be in part due to our incomplete observations on *V. mongolica*. However, the latter species seemingly does not use such an elaborate trick as does *V. orientalis*. Probably *V. mongolica* depends more on its swiftness and agility to catch honeybees, which also makes precise observation difficult.

Finally Ishay *et al.* write "....Hornets deplete bee hives during the summer and may on occasions totally destroy entire apiaries." After the hornets dispose of the sentry bees at the hive entrance, they invade the hive proper and gobble up the adult bees, the young and any food lying about". Once occupying the hive, hornets do not leave until they exterminate it. During this time, some sentry hornets stay at the hive entrance and defend the hive against the hornets of other colonies". This trait, the occupation of hives, resembles the mode of attack by *V. mandarinia* on bee hives as described in the next section.

5. Attack by *Vespa mandarinia* on hives of the European honeybee

5.1. *Phenology of visits to apiaries by* V. mandarinia: In contrast to other *Vespa* species, visits by *V. mandarinia* to apiaries is seasonally well delimited. In middle May, some queens visit apiaries together with queens of *V. mongolica* and *V. crabro*. Okada (1961 b) recorded hunting of bee workers by these queens twice but so far we have not observed hunting by them. Such queens are mostly uninseminated ones with degenerated ovaries (cf. **3. 2.**). Thereafter, virtually no queens or workers visit apiaries until early August although visits by other species, notably *V. mongolica*, are not rare. In early August the nests are at the end of the cooperative period or the start of the polyethic period in the annual cycle (cf. **3. 2.**), with 70~80 workers per nest. After the first visit in early to middle August, visits to apiaries become constant in late August and gradually increase thereafter, reaching a peak in middle September to middle October, with the number of daily visits 30~50 hornets per apiary (estimated from the sum of the numbers of hornets daily killed and trapped), a level easily noticed by the amount of monthly correspondences to the editors of bee journals. A well marked phenology is shown in Fig. 5, giving four years' records of daily catches prepared from the samples offered

by Mr. Y. Asai, in Ômuta, Kyushu, mostly consisting of *V. mandarinia*, with an admixture of a few *V. crabro* and *V. analis*. In September to October the numbers of both workers and combs reach maxima and lower combs contain larvae of sexuals, which must require a large quantity of protein food, in spite of the decrease of the prey in the field. Probably this may partly explain the concentrated visits by *V. mandarinia* to apiaries in these months.

The deficiency of protein food is solved in other species as follows: 1) *V. tropica*: Rearing of sexuals ceases in middle to late August, in parallel with the completion of brood rearing of *Polistes* wasps, the principal food source. 2) *V. crabro*: Following *V. tropica*, rearing of sexuals ceases in early September. 3) *V. analis*: Sexuals emerge in September to October. This species is agile. In autunm, hunting of small vespid adults, *Vespula lewisii* and *Polistes* spp. by this species is frequently seen in bushes. 4) *V. mongolica*: Rearing of sexuals continues later than in *V. analis* and emerged sexuals are seen until December. But this species is very agile, being able to catch various insects. Hunting of dipterans and hymenopterans is frequently seen in autumn on flowers. In contrast to these species, *V. mandarinia* is active to November, but slow in movements, unskillful at capturing agile insects. The prey so far observed in the field are mainly large caterpillars and large web spiders.

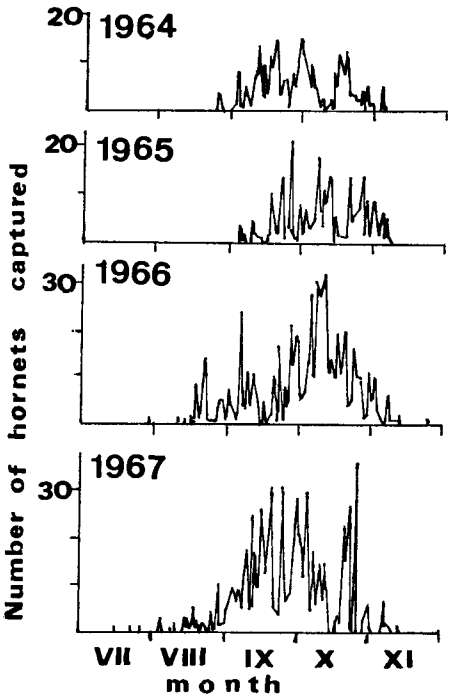

Fig. 5. Phenology of hornets captured by traps attached to hives. Prepared from the samples offered by Mr. Y. Asai (mostly *V. mandarinia*, with a few admixture of *V. crabro* and *V. analis*).

However, why *V. mandarinia* does not visit apiaries until 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. Or, the attack on apiaries may be released only after a sufficient number of workers have emerged. At the present there is little concrete evidence to test these assumptions.

5.2. *Attack I. Hunting phase*: During the season of visits by *V. mandarinia*, many beekeepers adopt some devices to defend their apiaries. The following observations were made without practicing such protective devices, supplemented with observations at protected hives. The attack by *V. mandarinia* is divided into three successive phases, hunting, slaughter and occupation.

The behavior of *V. mandarinia* in the hunting phase is basically the same as that of *V. mongolica* and other species. 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 by legs in the air and immediately bites it to death.

In the hunting phase, therefore, each worker repeats a chain performance of visiting→waiting→catching one bee→preparing a meat ball from the prey's mesosoma→carrying back the ball to the nest. At a hive which counter-attacks weakly, 2~5 hornets may visit synchronously or alternately. They invariably repeat the same performance, never leaving the corpses of bees in the apiary as in the next phase.

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 and the hornets' nest. When the apiary is located near the hornet nest and receives constant visits by hornets of the same nest, the shift is nearly certain, while at an apiary remote from the outskirts of mountains and hills, where most hornet nests concentrate, the frequency of visits is low and the shift to the next phase is rather rare.

The flight radius of *V. mandarinia* is on the average 1~2 km, reaching 8 km in the maximum. The distance between a nest and apiaries attacked is mostly 1~2 km (max. 2.5 km) (Ikeda, pers. comm.) and serious damage appears mainly at apiaries located less than 1 km from hornet nests (Kojima 1950). On departing from nests, *V. mandarinia* workers tend to soar once over the canopy of trees before changing to horizontal flights.

So long as the attack remains in the hunting phase, the damage to hives does not exceed much that by *V. mongolica* or is often inferior because of the lower frequency of visits reflecting its smaller nest population, and less agile behavior than *V. mongolica*.

5.3. *Attack II. Slaughter phase*: Once the attack shifts to the second phase, the behavior of hornets changes drastically. Not visiting different hives alternately as in the hunting phase, they concentrate attacks on a particular hive, ignoring others even if placed side by side. If one captures a hornet at this phase and liberates it near the apiary, she immediately returns to the victim hive to recommence the attack. Once chosen, the victim hive is not altered throughout this and the next phase.

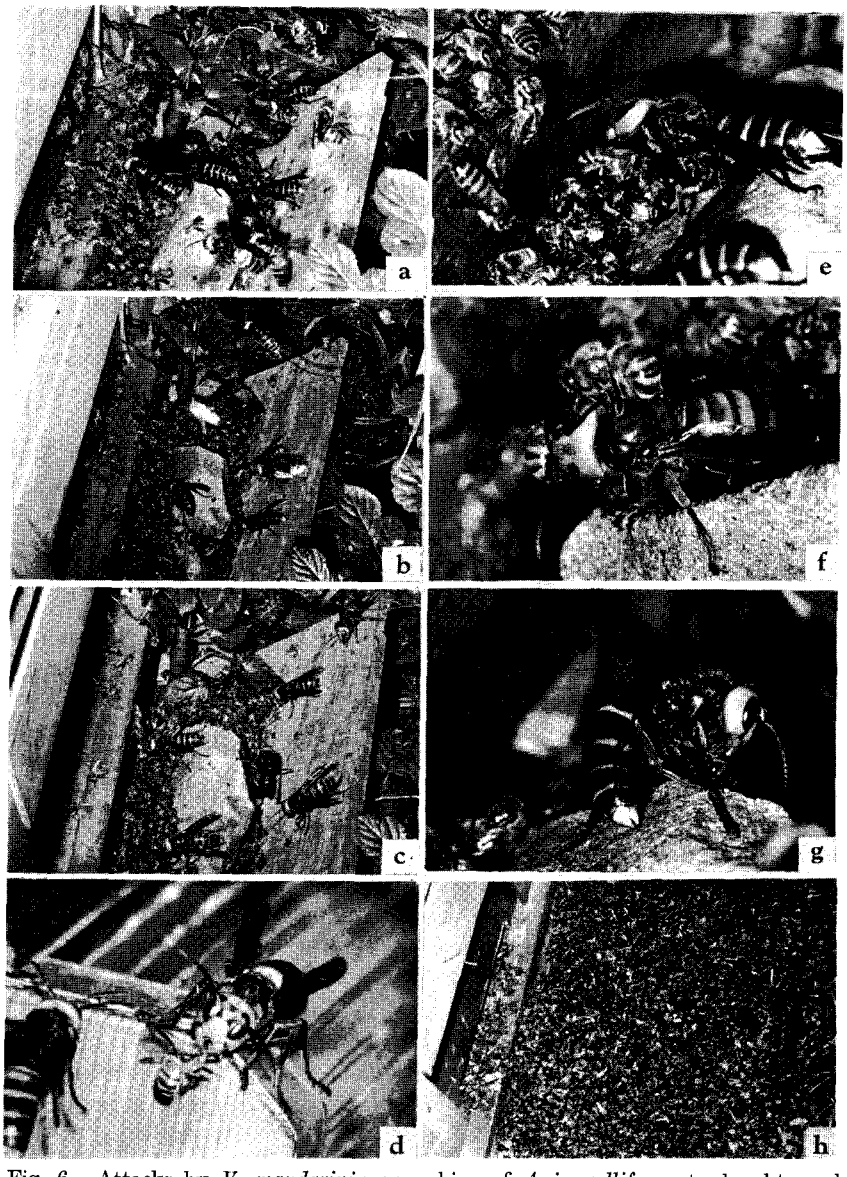

Fig. 6. Attacks by *V. mandarinia* on a hive of *Apis mellifera* at slaughter phase. a~c. Sequence of slaughter phase with gradual decrease of defense and increase of bees killed by hornets, d. Hornet crushing the head of a bee, e. Hornet attempting to pull a bee, f. Hornet biting a bee and receiving the counter-attack of another, g. Hornet biting a counter-attacking bee, h. Result of a slaughter, photographed after removing hornets.

The attack in this phase is a simple repetition of slaughter (Fig. 6). Usually staying near the hive entrance, each hornet bites to death each bee approaching her for counter-attack. 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 by legs, bites her to death, throws down her corpse and returns to 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, up to 50, though they do not work co-operatively. 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 day, hornets return to their nest at sunset but reattack the victim hive on the next day in the early morning. Once ten hornets in the slaughter phase were individually marked. All of them returned on the next day to the victim hive.

As shown by individual marking, 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 at the inicial part of the phase and mostly practiced by bees of guard or foraging ages. But foragers returning to the hive often do not participate in its defense and 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 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 appears as slaughter continues, resulting in the appearence of frequent and persistant food exchange (cf. **3. 4.**) at the apiary. In extreme cases, the hornets starve to death during prolonged slaughter.

The number of bees killed by hornets varies according to sizes of victim colonies, number of hornets, and intensity of counter-attacks. In southern Japan, the hives managed by the non-migratory apiculture involve 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. Death of hornets during the slaughter phase are mostly only one to two. In one concrete instance, about 25,000 out of 30,000 inhabitants were killed during three hours by 30 hornets while only two hornets were killed by bees (Fig. 6. h.). This means that each hornet killed approximately one bee every fourteen seconds.

The causal mechanism underlying the shfit from hunting to slaughter phase is yet unknown. As the shift usually appears after hornets have received intense

counter-attacks, the latter must release the change of their behavior. However, the shift develops only when more than one hornet of the same nest participate 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 at hunting phase favors 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 shfiting 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 favor this assumption, but the problem is still open to critical studies.

5.4. *Attack III. Occupation phase*: After the cessation of defense by slaughter and escape of survived bees, hornets successively enter into the victim hive and occupy it. They pay little attention to some bees still surviving in the hive. Once slaughter phase is attained, it invariably proceeds to occupation phase unless artificially inhibited. Within the hive each hornet walks around combs, opens a cocoon and pulls out the pupa. Keeping it with mandibles, she flies away to a branch near the apiary, 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. But it ceases on the next day, probably because of putrefaction.

In this way, the occupied hive is continuously visited by a dozen to several tens of hornets in daytime for several days to a half month. Often some individuals pass the night in the hive, not returning to their own nest.

Hornets in the occupation phase change their disposition. The occupied hive is guarded by some individuals sitting at the entrance. 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, hornets do not make such attacks to men during the hunting and slaughter phases, so that they can be beaten to death with wooden sticks, etc. 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 and threatens them by a particular loud clicking produced by rapid opening and closing of the mandibles. This clicking is produced in all Japanese hornet species at or near their nests, though one of us (M. M.), could not hear it in *V. basalis* in Formosa, 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 occupied and tree sap sources frequently visited. This indicates its well developed territorial defense. The

relative aggressiveness of various species to men at or near their own nests is ordered: *mandarinia*≫*mongolica*≥*crabro*>*analis*≫*tropica*.

Although occasional entries into hives are recorded for some other hornet species (cf. **4.3.**), a lasting occupation of victim hives is previously recorded only in *V. orientalis*. From the description by Ishay *et al.*, the presence of a distinct slaughter phase in this species is not clear. It may be interesting to know 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 our observations go, hornets destroy honey combs but rarely take honey to carry back it to the nest. As seen from the observations recorded in the next section, the main aim of occupation must be predation on pupae and larvae. Most observation cited in section **4** on other *Vespa* species confirm the preference for the muscular mesosoma of the prey. This is in marked contrast to visits by *Vespula lewisii* to apiaries; this species seeks mainly the stored honey. Free (1970) showed that meso- and metasoma of honeybees are equally preferred by the European yellow-jackets, *Vespula germanica* and *Vl. vulgaris*. This might indicate that *Vespula* is less predaceous than *Vespa*. As shown in **3.1.** and **4.1.**, *V. mandarinia* workers are specially 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 for the latter. These facts suggest that the stored honey does not form a principal objective of the hive occupation.

6. Attack by *Vespa mandarinia* on other vespid species and the Japanese honeybee, *Apis cerana*

Attack by *V. mandarinia* are not limited to the European bee but are made also on nests of other winged social Hymenoptera. On the other hand, at tree sap, *V. mandarinia* chases away but does not hunt other congeneric species and other insects.

6.1. *Attack on nests of other social wasps*: Complete observations from the start to the finish of an attack are scarce. The following description was made by combining fragmentary records and information from other persons. All attacks on nests of other social wasps were observed in September and October. Since the start of attacks on honeybee hives, *V. mandarinia* workers frequent eaves and similar places in search of nests of other social wasps. This behavior does not appear before mid August. Some *Polistes* nests built in the places apparently noticed by cruising *V. mandarinia* workers did not receive attacks before that time. Since November, *V. madarinia* workers forage mainly carbohydrate food so that attacks on both bee hives and wasp nests cease.

All five species of *Vespa* observed attack nests of *Polistes* wasps and pillage immatures, mainly pupae, with the following frequency order: *tropica*≫*mandarinia*≥

mongolica≥*analis*≥*crabro*. Except for *V. tropica*, the species highly dependent on *Polistes* (cf. Sakagami and Fukushima 1957 b), hornets attack mostly nests after emergence of sexuals, and *Polistes* adults, even in such large species as *P. jadwigae* Dalla Torre, escape from nests with no counter-attack, so that serious damage to *Polistes* population is mainly caused by *V. tropica*. Attacks by *V. mandarinia* on *Polistes* nests are relatively rare, mainly performed after the emergence of sexuals. These sexuals and still surviving workers abandon the nests when attacked by *V. mandarinia* and never return more, though they return after attacks by *V. tropica*. Attacks by hornets including *V. mandarinia* on *Polistes* nests do not have phase differentiation due to small nest size and escape of adults. The attack is regarded as a brief occupation made by solitary hornets which behave as in the hunting phase without slaughter.

Attacks on *Vespula* and *Vespa* nests are so far observed only by *V. mandarinia*. In *Vespula* hitherto only cases in the occupation phase have been observed (Fig. 7a) but cases interrupted at hunting phase may occur. 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 mandibles, not by sting. The counter-attack by *V. lewisii* seems not so severe as by *Apis mellifera*. Usually few deads of both predators and prey are found at the nest entrance. In a nest occupied by about 20 *V. mandarinia* workers, several tens of *V. lewisii* were still alive in the nest and departures and returns of a few *V. lewisii* workers were observed. It is an open question whether the slaughter phase is here so conspicuous as in case of the honeybee.

Attacks on nests of other hornet species start with the hunting phase. *V. mandarinia* suddenly pounces upon an individual victim at or near 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 in case of the honeybee. However, the attacked species, especially *V. analis*, occasionally kills *V. mandarinia* by counter-attack using the sting. In large nests of *V. mongolica* and *V. crabro* usually many workers take 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 combats are naturally much more severe than in attacks on *Apis mellifera*. Several workers of victim species or sometimes only one in *V. analis* confront each *V. mandarinia* in flight or on the nest entrance (Fig. 7, b). Two opponents fall down the ground and fight violently with each other, using mandibles, legs and stings (Fig. 7, c). The slaughter phase lasts several hours or continues to the next day. Numerous dead of the victim species and 20～30 of *V. mandarinia* left near the victim nest are carried back to the nest on the first day (Fig. 7, d), but not on the next day because of putrefaction. In all so far observed cases, the slaughter phase always proceeded to the occupation phase. *V.*

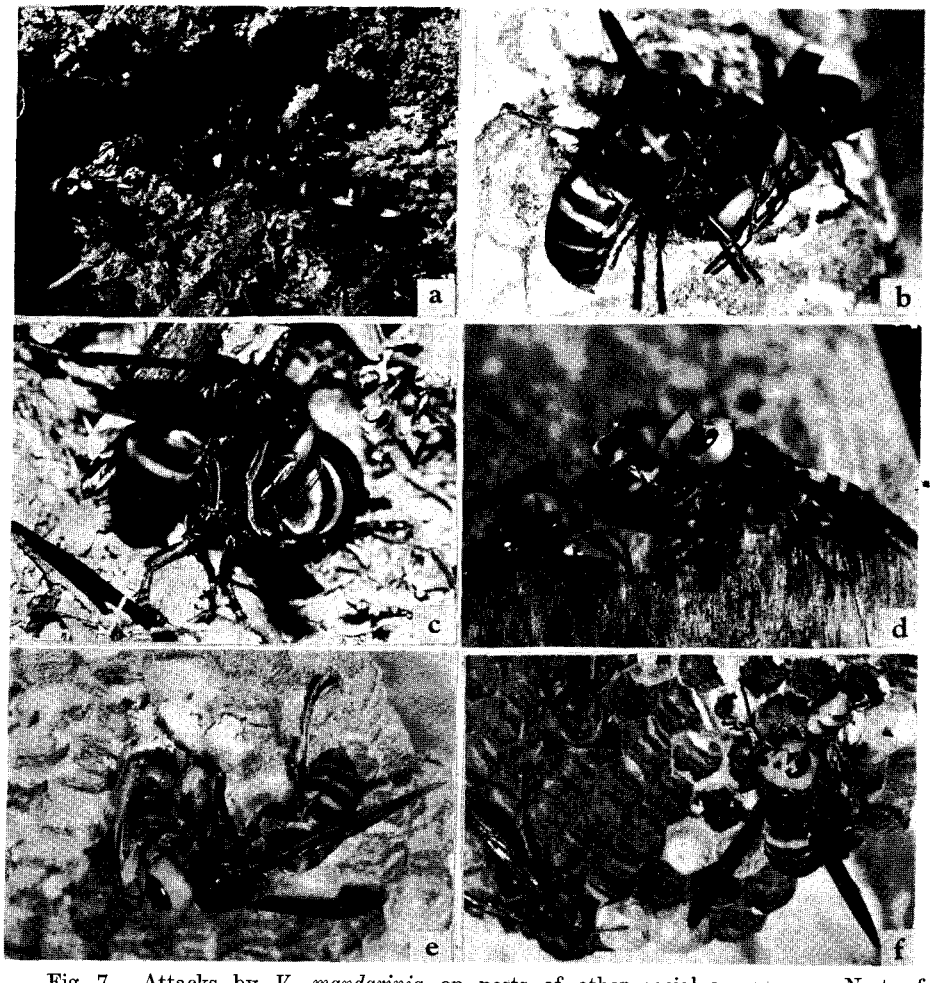

Fig. 7. Attacks by *V. mandarinia* on nests of other social wasps. a. Nest of *Vespula lewisii* occupied by *V. mandarinia* (Wings marked with white lacquer. Soil above the nest removed to take photo). b. Counter-attack by *V. analis* on *V. mandarinia* (left-below) on the nest of the former species. c. Ditto, *V. analis* killing *V. mandarinia* (right below) on the ground below the nest. d. *V. mandarinia* worker manipulating the dead of a nest-mate killed by *V. analis*, e. *V. mandarinia* worker pulling out a pupa in the occupied nest of *V. mongolica*. f. Ditto, two *mongolica* workers sitting aside without resistence.

mandarinia ignores adults of the victim species still remaining in the nest and procures the immatures (Fig. 7, e, f). As in case of *Apis mellifera*, the pupae, especially of the advanced stages, are preferred, while larvae are only partly carried back.

On the other hand, when the victim nests are too small, the owners abandon the nests and never return more as in *Polistes*. One interesting exception is cited:

10. August 1971. A small nest of *V. mongolica* was started inside a hut by an absconding swarm. (In this species, the majority of nests once perform such translocation during July to August). 15. Aug. There were 31 cells, 33 workers and the envelope about two thirds completed. 23. Aug. There were only the foundress and one worker. The damage given to the nest suggested the attack by *V. mandarinia*. No dead of both species was found on the ground below the nest. There were only eggs and first instar larvae in the nest so that the attack was probably rewarded. This was the earliest case of the attack by *V. mandarinia* on other social wasps.

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 period before the attacks by *V. mandarinia* intensify. Once its nests are discovered and attacked, it is certain that this mildest hornet making smallest nests is easily conquered by *V. mandarinia*. Two small nests reared by M.M. were attacked and occupied each by only three workers of *V. mandarinia*. 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.

6.2. *Attack on hives of the Japanese honeybee*: The foregoing description shows that nests of other social wasps are victimized by *V. mandarinia*. Only large nests of *V. mongolica* and *V. crabro* can resist the attack and inhibit it at the incipient stage of the hunting phase. Meanwhile, there is another social insect which developed an excellent defense against *V. mandarinia*: the Japanese honeybee, *Apis cerana cerana* Fabricius, the easternmost and largest subspecies of the Asiatic honeybee.

Since Tokuda (1924) it is well known that this species avoids the damage by retreating within nests at the arrival of *V. mandarinia* (Sakagami 1960). 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.

At the arrival of a hornet, departures from the hive abruptly cease. The shimmering, a warning sound characteristic to the species (Sakagami 1960), is repeatedly emitted in the hive. Homing foragers keep a distance from the hornet and quickly enter into the hive through holes remote from the enemy. By this rapid retreat with no solitary counter-attack, the hornet usually relinquishes her attempt and leaves. If the hornet persists, however, numerous bees appear from the entrances remote from it (Fig. 8). Never flying nor darting solitarily to the hornet as *A. mellifera* does, some bees approach the hornet, directing the heads to the enemy, raising their metasomal tips and vibrating the wings (Fig. 8, a). 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 entrances concentrate on the place (Fig. 8, b). About 10 ~ 15 seconds after the attack by the first bee, the hornet is covered thickly by several tens to several hundreds of bees (Fig. 8, c). Shimmering in the hive repeated since the arrival of the hornet ceases and departure of foragers recom-

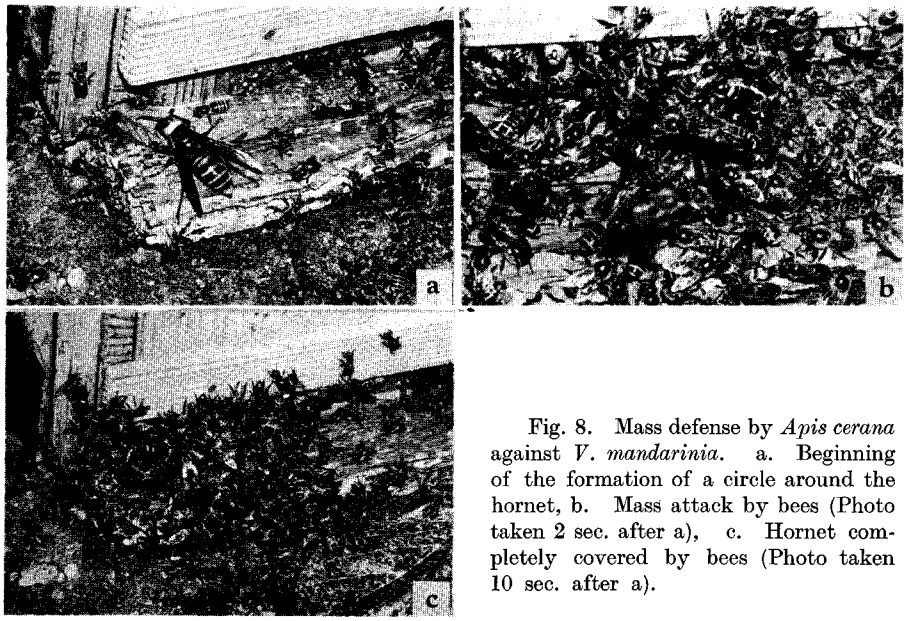

Fig. 8. Mass defense by *Apis cerana* against *V. mandarinia*. a. Beginning of the formation of a circle around the hornet, b. Mass attack by bees (Photo taken 2 sec. after a), c. Hornet completely covered by bees (Photo taken 10 sec. after a).

mences. 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. So far as our observations go, virtually no bee died through the defense. 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 inicial part of the hunting phase. The hornet either is killed or abandons the attack which does not develop into its subsequent phases. We have had the opportunities to observe only a few instances of the mass defense described above. But the lack of sufficient observations is just due to the rarity of catastrophic damge by *V. mandarinia*. According to the experience by several beekeepers and one of us (M. M.), *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 M. M. 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 colonies at the same time, invariably informed the absence of catastrophic damage by *V. mandarinia.*

Naturally we do not insist that the defense by *A. cerana* is always successful. 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 a mild damage is cited:

22 October 1972. Three workers of *V. mandarinia* flying around in front of a *A. cerana* colony were noticed. The bee colony 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 100 m apart. The workers of this nest exterminated during September and October two nests of *V. mongolica,* two of *V. analis* and one of *Vespula lewisii.*

Nevertheless, it is certain that *A. cerana* developed two fairly effective defensive techniques, both not possessed by *A. mellifera,* one being passive, the absence of solitary counter-attacks, and the other, active, a rapid mass attack, through a long contact with *V. mandarinia.* This skillful defense is sharply contrasting with its inability to resist the 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 three species during a century.

As cited in **4. 3.** serious damage to bee hives by hornets, including *V. mandarinia magnifica,* are recorded in India (*Apis cerana indica*), Indochina (*A. c. javana*) and Afghanistan (*A. c.* ssp.). Several possibilities exist to explain the discrepancy between these records and observations in Japan: 1) Lower defensive ability in souther populations of *A. cerana* against *Vespa.* 2) Presence of some efficient hunting behavior in *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 to study the use of appropriate hives, especially those with the entrance not too widely made.

Recently Kloft and Schneider (1970) described a defensive behavior of *A. cerana* ssp. in eastern Afghanistan to *Vespa* sp.: At the arrival of a hornet, 30 bee workers from a dense mass at the nest entrarce, each changing the 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 catches only bees leaving the defensive mass. In general the observation cited corresponds to ours but the inicial retreat and mass counter-attack observed by us are not mentioned. Considering this absence of description, together with the serious damage of *A. cerana* received by *Vespa* in the same area (cf. **4.3.**), the defensive behavior in the Afghan population seems as if less perfect than in Japan. It is important to make further comparative observations on the defensive behavior of *A. cerana* in various areas.

Ishay *et al.* 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 instances, 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 belonging to *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 we have so 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 such discrete presence of a behavior 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 behavior both of hornets and honeybees may throw light on reciprocal evolution of attack and defense mechanisms in these insects.

A few words are added to as to attacks by other hornet species on *A. cerana*. *V. mongolica* occasionally hunts individually *A. cerana* foragers in the air and brings victims to its nest after preparing a meat ball as described in **4.2.** The mass defense by *A. cerana* may be more effective to *V. mandarinia*, which cannot hunt *A. cerana* in the air but waits it near the hive. But visits to nests of *A. cerana* by *V. mongolica* are less frequent than to nests of *A. mellifera*. No visits by *V. analis* and *V. crabro* to nests of *A. cerana* have so far been confirmed, even though four nests of *V. analis* were once kept by M.M. 5 ~20 m apart from a *A. cerana* hive. On the other hand, hunting of *A. cerana* by these hornet species out of the nest site is plausible, especially by *V. analis*, which has a trait to hunt various wasps and bees, for instance, *Polistes*, *Vespula*, *Megachile*, etc., though actual hunting of *A. cerana* has hitherto not been observed.

7. Control of hornets practiced in Japan

The records on damage by *Vespa* cited in **4. 3.** were mainly procured from "Bee World" and "Apicultural Abstracts". Although we did not make a precise calculation, the number of articles on hornets must surely be less than 5% of all articles on enemies and diseases of honeybees cited in these periodicals. We also checked all articles on bee enemies and diseases appearing in "The Japanese Bee Journal Monthly", the most representative bee journal in Japan (Vol. 1, 1948 ~ Vol. 23, 1970), and obtained the following statistics: Hornets 58, miscellaneous 32, foulbrood 23, mites 14 poisoning 14, *Nosema* 4, toads, spiders each 2, ants,

hawkmoths, amoeba, asilid flies, rats, bears each one, in total 155. The articles on hornets occupy the first rank and more than one thrid of the total. This is sufficient to show how serious the hornet problem is for Japanese apiculture. In this final section, diverse control methods practiced in Japan are presented based upon the articles mentioned above.

Control methods of hornets in Japan are classified into: 1) Beating to death, 2) Removal of hornet nests, 3) Bait trapping, 4) Mass poisoning, 5) Trapping at hive entrances, 6) Protective screen. Most of these devices have been invented by beekeepers not in governmental institutes. Correspondingly, the efficiency of the devices is inevitably not well measured with control tests. As we have so far never engaged in the control of hornets, we are not always sure of the real efficiency of the devices described below, though some of them seem quite effective when used appropriately.

7.1. *Beating, nest removal, bait trapping and mass poisoning*: The beating to death of hornets visiting apiaries is the method practiced since the beginning of the modern apiculture using *A. mellifera*, and is still widespread in Japan. Hornets are crushed with wooden sticks with flat heads, etc. As described in **5.4.**, this procedure is efficient in the hunting and slaughter phases, because hornets in these phases do not counter-attack and a large and relatively clumsy *mandarinia* worker is an easy target. One problem with this method lies in the expense of time or payment to employees. The other is that *V. mandarinia* may enter the slaughter phase and exterminate a hive during a brief time in the absence of the caretaker.

Once discovered, the destruction of hornet nests is not difficult by applying poisons or fire at night. But to discover its subterranean nests, often remote from apiaries, is not always easy. In Japan the immatures of yellow-jackets, *Vespula* spp., are esteemed in some areas, especially in Nagano Prefecture, where they are collected and canned for sale. The method commonly adopted to discover their nests is to present a piece of frog or fish meat attached to a cotton ball to a foraging wasp and to pursue her flight course. A similar practice is occasionally adopted for *V. mandarinia*, but is not always successful because of its large flight range.

Bait traps are placed at apiaries. Most are in principle provided with a narrow, one-sided hole from which return is difficult once the hornet is in the *cul-de-sac*, though honeybees can freely pass through the mesh. Two types of bait traps are shown in Fig. 9: A is the application of Miki's hornet trap explained in **7.2.**, by closing the back with a wooden board (Fig. 9 A, b). The baits used are diluted mellet jelly solution or crude sugar solution with admixture of intoxicants, vinegar, fruit escence, etc. (Fujii 1967, Hayashi 1953, Tawara 1966).

Mass poisoning has been proposed by Tokuda (1952～'64, cf. also Sakai 1959, Takahashi 1964). The procedure is to catch the hornet at the apiary and to liberate her after feeding her with sugar solution or giving her a dead bee or hornet, both poisoned with diluted lead arsenate, malathon, etc. and to await the spread of

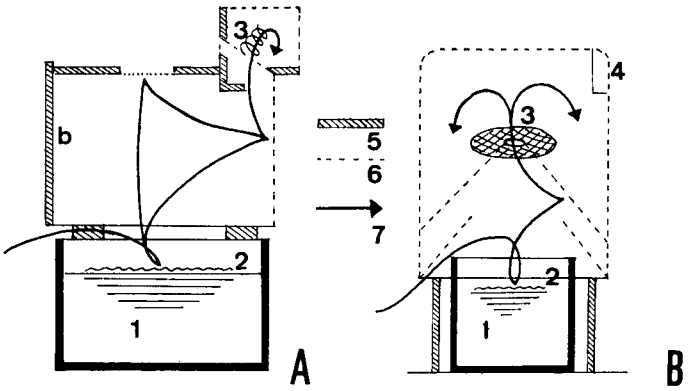

Fig. 9. Bait traps placed at apiaries. A. Improved Miki's trap placed on bait container after closing the back (b), B. Large bait trap for intensive catch (both from Fujii 1976 with slight modifications). 1. Bait, 2. Paper or other platform to prevent drowning, 3. One-way trap hole leading to *cul-de-sac*, 4. Hole to remove dead hornets, 5. Wooden parts, 6. Wire lattice passable by bees but not by hornets, 7. Flight course of hornets.

toxic action through trophallaxis in the nest. The method is in principle reasonable but the effect is still not sufficiently tested.

7.2. *Trapping at hive entrances*: The hornet trap is a memorable invention by Japanese beekeepers in their hundred years' fight against hornets. As briefly reviewed by Aoki (1950), the earlier types were probably deviced as protectors. Through successive improvements, its aim as more trap than protector has gradually been stressed.

As shown by a standard type illustrated in Figs. 10, A and 11, a, b, the trap is attached to the front of the hive. It consists of a main compartment and a capturing chamber placed on the top of the former. The front of the main compartment and the front and top of the capturing chamber are made by a lattice, which allows the free passage of bees but not of hornets. The hornet enters in the main compartment (Fig. 10, A, 2) through the entrance slit in the lower part (A, e). Receiving the counter-attack or catching a bee, the hornet always flies back and collides against the frontal lattice (8). Deprived of hunting urge by the collision, she seeks to escape upwards and ultimately enters the capturing chamber (6) through a trap hole (5) from which she has difficulty to return. The corpses of hornets are later removed from the back of the chamber (7).

Obviously the trap does not always function efficiently. Some hornets escape through the front entrance (e). Some others do not enter the trap and wait the bees at its top or front. The worst is that many bees make counterattacks at the

outside of the trap (Fig. 11, c, cf. also Fig. 6, d), which occasionally evokes a considerable loss of bees of outdoor work ages, even if catastrophic slaughter is decreased and subsequent occupation is inhibited. Kiribayashi (1950) enumerated the conditions necessary for an effective trap as follows (partly modified by us): 1) Entry of hornets without hesitation. 2) Rapid passage of hornets into the capturing chamber. 3) Minimum escape of hornets once trapped. 4) Minimum solitary counter-attacks by bees outside of the trap. 5) Minimum disturbance for the traffic of foraging bees. 6) Simple, not bulky and easy to install, to manipulate and to remove. 7) Not expensive. Thus, the efficiency of a trap is intimately linked with

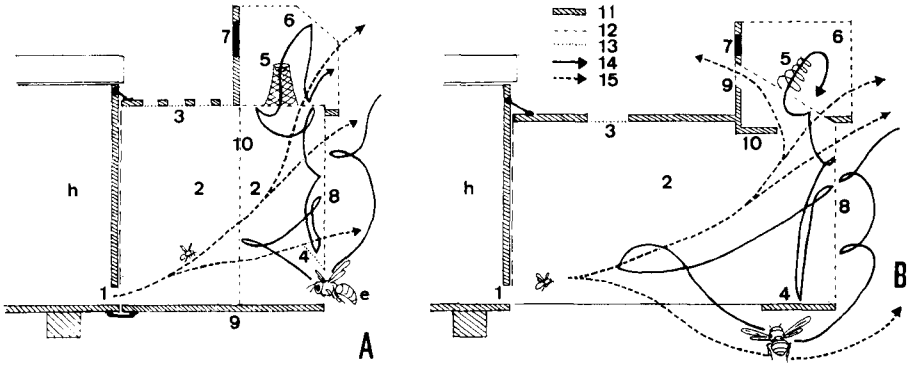

Fig. 10. Mechanism of hornet traps. A. Standard type, B. Improved Miki's type. h. Bee hive, e. Front entrance (only in A), 1. Hive entrance, 2. Main compartment, 3. Skylight, 4. Plate inhibiting escape of hornets, 5. Trap hole, 6. capturing chamber, 7. Hole to remove dead hornets, 8. Front lattice, 9. Bottom board in A, bee exit in B, 10. Intermediate lattice in A, blind board in B, 11. Wooden parts, 12. Wire lattice passable by bees but not by hornets, 13. Ditto, not passable by bees and hornets, 14 and 15. Flight courses of hornets and bees.

behavioral interactions between predator and prey. Consequently, an attempt to remove one defect often provokes another. To entice hornets into the trap, the latter must be sufficiently skylighted, which, however, increases the perception of the enemies and subsequent counter-attacks out of the trap by bees.

Considering various merits and defects, Mr. S. Miki deviced a trap without bottom board, which was later improved by some beekeepers, especially by Fujii (1965) as shown in Fig. 10 B and Fig. 11, d. Although we are not well qualified to appraise the relative efficiency of various traps, Miki's bottomless trap seems to be quite effective, judging from the opinions of many beekeepers, mainly for the following reasons (Fujii 1965, partly modified): 1) Removal of the bottom board facilitates entry of hornets. 2) It also facilitates passage of foraging bees so that the trap can be attached to the hive before the hornet season, without too much

decreasing foraging efficiency. 3) It also decreases counter-attacks by bees which dart from the bottom board. 4) The capturing chamber is invisible from bees at the hive entrance so that their darting, released by hornets within the chamber, is avoided. 5) The sloped (45°) bottom of the capturing chamber and its trap hole made by a coiled wire, which vibrates when a hornet in the chamber perches thereupon, inhibit the escape of hornets. 6) Removal of the intermediate lattice (Fig. 10A, 10) decreases the flying to and fro of confused hornets in the main compartment, which releases counter-attacks by bees.

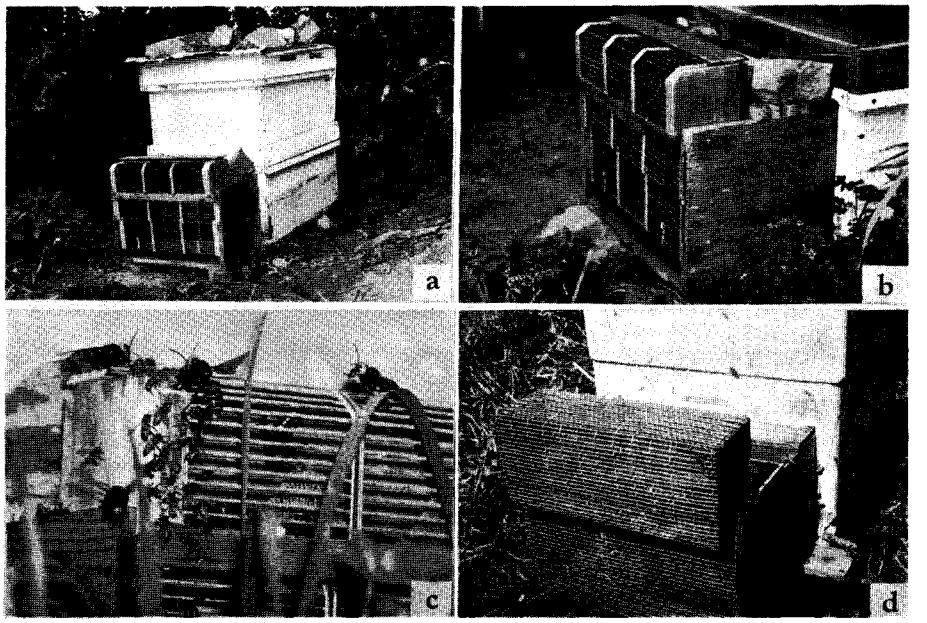

Fig. 11. Hornet traps attached to bee hives. a and b. Standard type, c. Slaughter by hornets of counter-attacking bees on standard type trap, d. Improved Miki's trap. (d, Photo by Mr. K. Fujii).

To prepare the lattice, rectangular meshes are preferred to square ones to make the passage of bees easy. The optimum size of the mesh is vertically 5.3 to 5.5 mm in all hornet species including small workers of *V. mongolica* are considered, though it can be widened to 7.0 mm for *V. mandarinia* alone.

Although often less efficient for small and agile *V. mongolica*, the improved trap mentioned above is fairly effective to catch *V. mandarinia*. However, to install it on all hives of an apiary is expensive and decreases both foraging efficiency and routine management efficiency. Therefore traps are often used in combination with other devices, especially the protective screens described below.

7.3. *Protective screens*: This procedure is in principle to create some obstacles in front of hives, releasing the vigilance of hornets and inhibiting their approach to hive entrances as well as disturbing the perception of hornets by bees which causes their departure for counter-attack.

The simplest way is to leave weeds in front of hives, to hang a screen such as cloths, newspapers, etc. (Fig. 12 A) or cover hive entrances with wire or fishing nets (Fig. 12 B). To confine the passage of bees at the higher entrance alone

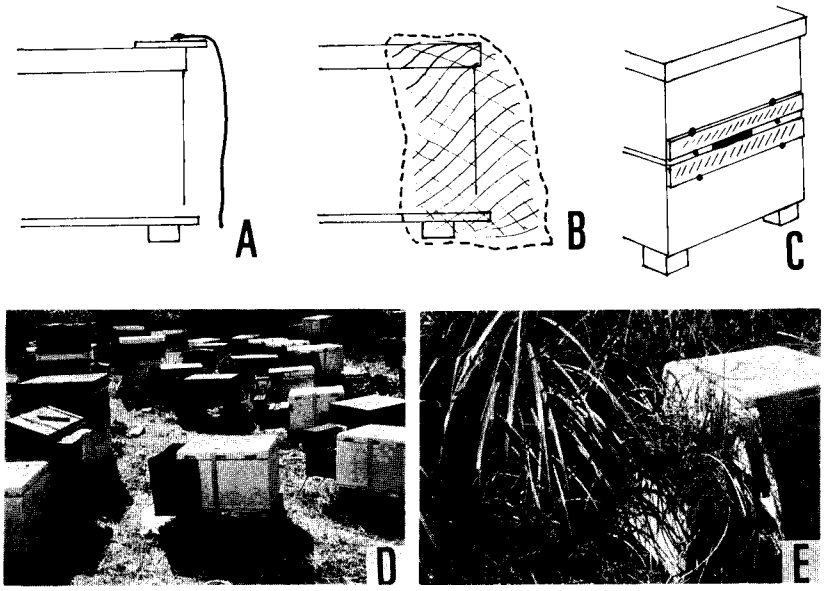

Fig. 12. Various types of protective screens. A. Simple screen hung down in front of hive, B. Fishing net covering hive front, C. Glass plates put above and below hive entrance, D. Vertical screen put in front of hive (At center and back. At right, hives with Miki's traps), E. Vertical screen filled with weeds (Photos D and E by Mr. K. Fujii).

and to put glass plates above and below the entrance (Fig. 12 C) can also inhibit alighting on and hunting by hornets there to some degree. Fujii (1967) deviced a simple vertical cloth screen installed in front of hives (Fig. 12 D). The screen is brought closer to the hive according to the intensity of hornet visits, down to the minimum distance of about three times wider than the hornet's body length.

However, all these screens gradually become less effective to experienced hornets, which stay on these obstacles and catch bees, either those making counter-attacks or those leaving from or returning to hives with decreased flight velocity. Therefore, the combined use of hornet traps and protective screens is often recommended. This forces hornets to avoid protected hives and to con-

centrate to the hives equiped with traps. In the combined use of the improved Miki's trap and vertical screens, the synergism of both, the avoidance to the screen and concentration on the trap, is effective only at the distance of 1 m, so that about 10 traps and 40 screens are required for 50 hives. (Fujii 1967, cf. Fig. 12 C). Later Fujii (1969) proposed to put weeds in the vertical screen (Fig. 12 E). According to him, the screen filled with weeds can function independent of traps and the number of traps can be decreased to five to 95 screens for 100 hives. However, putting weeds into all screens often takes much time, so that a simpler hanging screen is also being tested in combination with traps (Fujii, person. comm.).

By the application of various devices mentioned above, the damage by *V. mandarinia* can be decreased considerably, though control is still far from satisfactory. On the other hand, visits by *V. mandarinia* to apiaries are gradually decreasing in some areas in Japan (cf. **4. 2.**). In such case, increased visits by *V. mongolica* are reported by some beekeepers. Although it is still premature to conclude, the replacement of *V. mandarinia* by *V. mongolica* as main bee hunters is not impossible in future, when frequent visits to apiaries, agility, and populous nests of the latter species are recollected.

Concluding remarks

The subfamily Vespinae, certainly occupying a summit of vespid evolution, contains only three genera. Leaving *Provespa*, a small genus confined to S.E. Asia, aside, the other two prosperous genera developed different modes of life though with a considerable overlap. *Vespa* increased the body size and predaceous habit and is more successful in subtropical areas, whereas *Vespula* (recently often splitted into a few genera) is smaller, more omnivorous and mainly adapted to temperate climates. In contrast to *Vespula*, the bionomics of *Vespa* has so far been less studied in Europe, probably because of the small number of species and its highly aggressive disposition, in spite of the pioneer work by Janet (1903).

In the present paper a preliminary sketch of the bionomics of the giant hornet, *V. mandarinia*, was given in comparison with other Japanese species. Morphologically this species is regarded as specialized. Although many aspects must be corrected and supplemented by further studies, it is clear that the giant hornet is unique in its mode of life, too. Some nest characters seem superficially primitive, but many of them may better be interpreted as adaptations to its exclusively subterranean nidification, which is in itself a secondary specialization in vespid evolution. The most remarkable trait of *V. mandarinia* is the hunting of other social wasps and honeybees, attacking and often exterminating their nests. A presumed course of the evolution of this peculiar habit is briefly outlined below.

The large body size and enormously developed genae, which support powerful mandibular muscles, gave *V. mandarinia* a formidable ability to attack and to conquer other animals. By this ability, combined with an extraordinary

aggressiveness and a strong toxic action by the stout sting, *V. mandarinia* occupied an unrivalled position among insects and other small animals, at least in Japan. In compensation, however, its relatively sluggish movement made the capture of fugitive prey difficult, which was especially conspicuous in comparison with some agile species, for instance, *V. mongolica* 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*, which is nearly entirely dependent on *Polistes* wasps. Keeping its polyphagaous habit, *V. mandarinia* began to seek prey easy to catch. Among such prey there would be those making colonies, with a large amount of protein food concentrated there. However, the dependence on *Polistes* as in *V. tropica* was probably impossible for *V. mandarinia*, whose nests reach a large size, requiring a large quantity of animal diet. On the other hand, the defense by nest owners made no serious obstacle for *V. mandarinia*. Or, it had to be rather favorable to *V. mandarinia* if a 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 expeling 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 resistence of victims, even if with a loss of several to several tens nest mates, which were transformed to meat balls 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 at attack on *Polistes* nests and seemingly not well developed at attack on *Vespula* nests, whereas distinct at attacks on victims with severe counter-attacks, other hornet species and *Apis mellifera*. Its releasing mechanism is still unknown but certainly relates with a change of motivation, which is probably affected by intense counter-attacks and presence of nest mates. Its functional significance may be to facilitate the occupation of 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 as occupation of favorable tree sap sources, too. Such *property defense* is observed also in cleptobiotic stingless bees of the genus *Lestrimelitta* (Nogueira-Neto 1970, Zucchi and Sakagami unpub.). Compared with the attack and nest occupation by this professional robber bee, the attack by *V. mandarinia* is far less elaborated 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* confronted in Japan 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 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.

Summary

The bionomics of the giant hornet, *Vespa mandarinia* Smith (ssp. *latilineata* Cameron), a serious pest for Japanese apiculture, is outlined in comparison with that of other congeneric species. Peculiar habits are: 1) Exclusive subterranean nidification. 2) Conical and irregular comb surface and incomplete nest envelope. 3) Mating in front of nests. 4) Frequent extranidal trophallaxis, and 5) Attacks on nests of other social wasps and honeybees.

The attack consists of three phases, hunting, slaughter and nest occupation. It is assumed that the habit of attacking other social wasps was applied to bee hives since the introduction of the European honeybee, *Apis mellifera* Linné, into Japan. The principal cause of the catastrophic damage to hives is solitary counter-attacks by *A. mellifera*, which has no effective defense such as is possessed by the Japanese honeybee, *A. cerana cerana* Fabricius. Main procedures of hornet control practiced in Japan are briefly presented.

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