



Title	Preliminary Observations on the Life History of Two Polistine Wasps, <i>Polistes Snelleni</i> and <i>P. biglumis</i> in Sapporo, Northern Japan (With 9 Text-figures and 3 Tables)
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# Preliminary Observations on the Life History of Two Polistine Wasps, *Polistes Snelleni* and *P. biglumis* in Sapporo, Northern Japan<sup>1)2)</sup>

By

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(With 9 Text-figures and 3 Tables)

The studies on the polistine wasps can contribute to the comparative sociology of wasps in three ways: 1) Their relatively simple social structure is easy to analyse than in other advanced social wasps, 2) Their nests devoid of outer envelopes make precise observations and experimental analyses possible, without giving noticeable disturbance to the colonies, 3) Their nearly cosmopolitan distribution involving numerous species enables to realize an extensive comparative study among species inhabiting different climatic zones. There are a large number of papers dealing with their life system. But most detailed studies are confined to a few species inhabiting the southern part of the north temperate zone, for instance, *Polistes gallicus* (L.) in Europe. In Japan, too, precise studies have so far been made only in southern Japan (Morimoto, 1953~1959, Yoshikawa, 1957~1963), whereas no work has hitherto been published concerning the populations in northern Japan, nevertheless the modification of annual cycle due to severe climatic conditions is very probable there. As a first approach to the study of their life system in northern Japan, the writer made some preliminary observations upon two species, *P. snelleni* and *P. biglumis* in the vicinity of Sapporo. The observations were carried out with a relatively small number of colonies and no detailed functional and ethological analyses were undertaken. But he believes that the result obtained can give the outline of their life history under local condition.

The descriptions are mainly based upon the periodical observations made at the foot of Mt. Hakken-zan from April to October, 1968 made at irregular intervals of 3 to 12 days. Additional data taken during 1962~1968 at Tsuneji-zawa, Bankei and Hoheikyo, all in the vicinity of Sapporo, are also incorporated when necessary. Nests observed at Hakken-zan first consisted of 38 nests of *P. snelleni* and five of *P. biglumis*. Caused by the subsequent evacuation or destruction, the number gradually decreased. The nests continued until the fall were only three in *P. snelleni* and two in *P. biglumis*. The following descriptions are given mainly based upon these successful nests. Some notes on the unsuccessful nests are given at the end of the results.

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2) Biology and sociology of *Polistes* wasps in Northern Japan, I.  
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Henceforth, the species are cited by their specific names alone. Their full names are listed here, together with the reference to the publications and the localities where the studies were made.

*annuralis*. *Polistes annuralis* (Linné). Rau, 1940, '42, Missouri, America.

*biglumis*. *Polistes biglumis* (Linné).

*chinensis*. *Polistes chinensis antennalis* Pérez. Morimoto, 1953~1959, Fukuoka, Japan; Yoshikawa, 1962, '63, Osaka, Japan.

*gallicus*. *Polistes gallicus* (Linné). Pardi, 1942, Italy; Deleurance, 1957, France.

*jadwigae*. *Polistes jadwigae* Dalla Torre. Yoshikawa, 1957~1963, Osaka, Japan.

(So far been erroneously spelled as *fadwigae* in most papers in Japan. cf. V. der Vecht, 1968).

*snelleni*. *Polistes snelleni* Saussure.

Before going further, the writer wishes to express his sincere gratitude to Prof. Mayumi Yamada and Dr. Shôichi F. Sakagami, Zoological Institute, Hokkaido University, Sapporo, for their kind guidance in the course of the present study. Cordial thanks are also due to Mr. T. Kawamichi, Zoological Institute, Hokkaido University, for his kind information upon the distribution of *biglumis* in Kitami Province, and to Messers. K. Hoshikawa and M. Sakurai for their unselfish and patient helps at tedious field observations.

## Results and Discussions

### 1. Habitat and nest site preferences

Throughout Hokkaido, both *snelleni* and *biglumis* are distributed in hilly or submontane areas, not in lowlands near or in urban areas. Therefore, these species are classified into the semi-highland type by Yoshikawa (1962 a). Vertical zones occupied are 200~400 m in *snelleni* and 200~600 m in *biglumis*, in and near Sapporo. Some nests of the latter species were found in Oketo, Prov. Kitami, at the altitude of 600 m in spite of severe climate.

Nests of both species are mainly found at the south or southeast facing slopes of herbaceous areas with sparse small trees and short weeds. Insolated road sides and rocky cliffs are also preferred. On the other hand, entirely bare grounds, mature forests and dense bushes of tall weeds such as giant knotweed (*Polygonum cuspidatum*) with little penetration of daylight are avoided, probably caused by adverse thermal condition (Michener and Michener, 1951, Morimoto, 1953 a, and Yoshikawa 1962 a).

Although the nest site preference of both species does not markedly differ in general, a tendency to the nest site segregation was observed in Hakken-zan when both species nested closely nearby. While most of *snelleni* were found under rocky cliffs (Fig. 1, A) rarely on twigs of trees, all four nests of *biglumis* on twigs of young trees (Fig. 1, D) never under rocky cliffs. On the other hand, at Tsuneji-zawa with *snelleni* alone, nests were hunged down on small trees, especially on afforested young larches (*Larix leptolepis*), or near the top of withered twigs cut off and gathered together in small piles. At Bankei with only *biglumis*, the afforested larches offered nesting sites as in Tsuneji-zawa. Finally, at Hoheikyo,

where *biglumis* was dominant along road sides, no clear nest site segregation was detected. It is open to the question whether or not the nest site segregation found at Hakken-zan was caused by the interspecific competition under high population pressure.

When attached on twigs of trees, nests are usually built 20~60 cm above the ground as far as no dense plant cover exists. If the ground is covered with tall

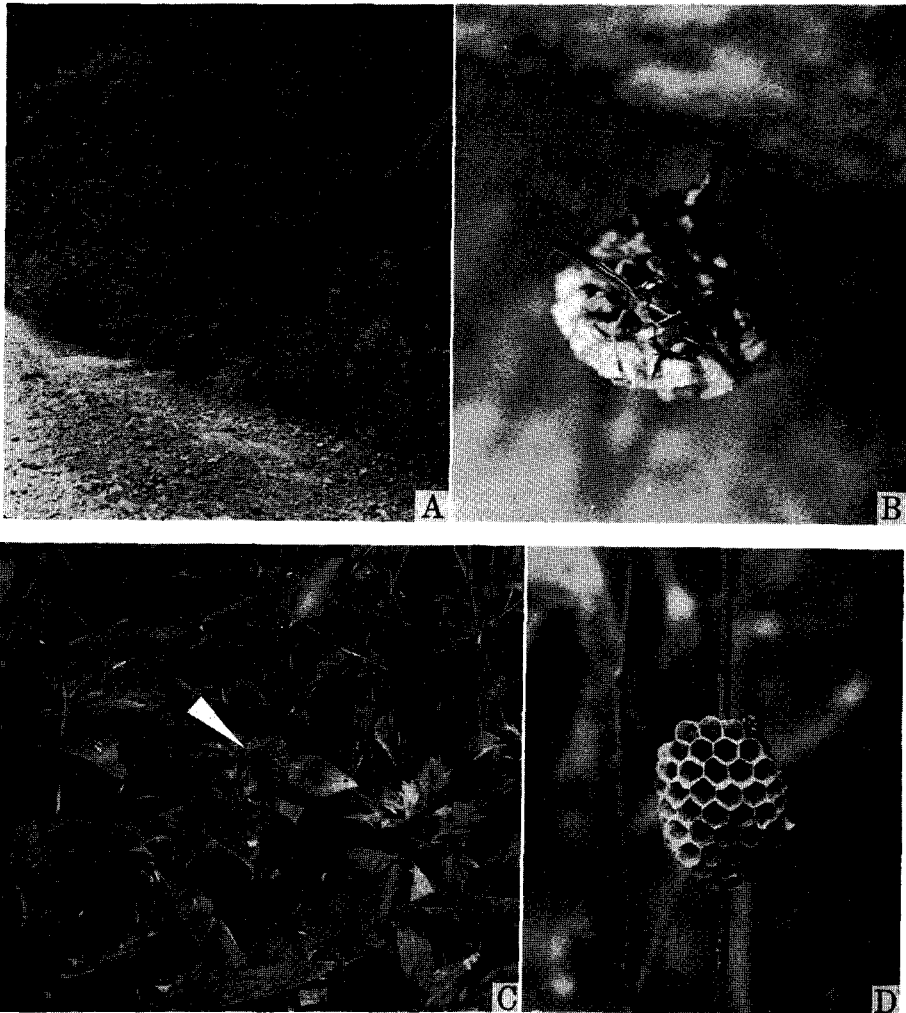


Fig. 1. A. Nesting site for *snelleni*. B. Early nest of *snelleni* under overhanging rock. C. Nest of *biglumis* made at the level above the top of the bamboo bush. D. Early nest of *biglumis*.

evergreen plants such as bamboos (*Sasa* sp.) of approximately 1 m high, nests are built at higher levels about 20 cm from the top of the plant cover (Fig. 1, C), but never exceeding 2 m above the ground. Trees frequently chosen for nesting are young larch (*Larix leptolepis*), elm (*Ulmus davidiana*) and alder (*Alnus hirsuta*).

The age of trees seems to have an important relation to the nesting habit of these wasps. Trees preferred for nesting are usually less than 2 m high irrespective of the species. Both in Tsuneji-zawa and Bankei, larch trees are now attaining 5~10 m high. Correspondingly, the population of polistine nests is seemingly in gradual decline. It is plausible that the original population is now in the course of dispersion, shifting to their favorable places such as road sides.

In case of rocky surface, the spaces under rock overhangs are preferred (Fig. 1, B). Although most nests in this site are not exposed to direct insolation for the most part of a day, the temperature raises considerably in daytime because of radiation of the heat absorbed by rocks.

In *snelleni*, both nest petiole and nest axis are made vertically. Correspondingly, the founding queens always make nests under horizontal supports, either twigs or rock surface (Fig. 1, B, and 2, B, D). In *biglumis*, however, both petiole and

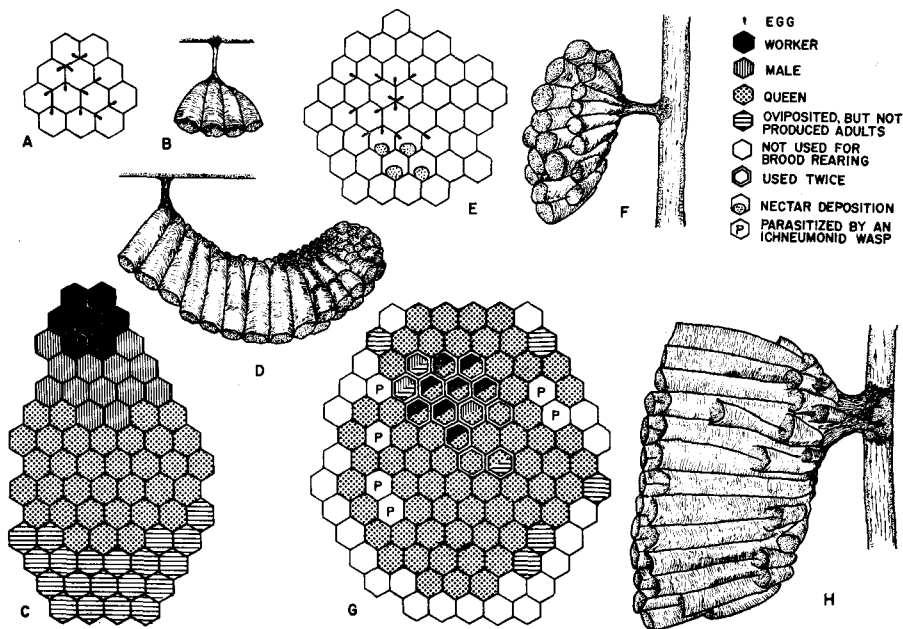


Fig. 2. Nest pattern of *snelleni* and *biglumis* showing morphological changes, oviposition pattern, and mode of cell utilization. A and B. Early nest of *snelleni* (Nest No. 6807) seen from below and in profile. C and D. Ditto, at later stage. E and F. Early nest of *biglumis* (Nest No. 6833). G and H. Ditto, at later stage. In Fig. G, about ten males, emerged sporadically within the area of cells producing young queens, are not indicated.

nest axis are horizontal, so that vertical surfaces are preferred for nest support (Fig. 1, D, and 2, F, H). In both species, the petioles are made nearly perpendicular to the supporting surfaces as in *chinensis* (Morimoto, 1953 b).

## 2. Annual cycle

Yoshikawa (1959, 1962 a) divided the annual cycle of *jadwigae* into six stages: 1) Solitary stage, 2) Superindividual stage, 3) Social stage, 4) Pre-hibernant stage, 5) Hibernant stage, and 6) Post-hibernant stage. Though the terms are not always appropriate for the population in northern Japan, this distinction is tentatively adopted in the present study. Three stages, pre-hibernant, hibernant, and post-hibernant stage, are not closely referred to because of the lack of sufficient observations.

### 2.1. Post-hibernant stage

In and near Sapporo, nesting places are covered with snow until early April to early May. The time of snow melting is early to middle April at the south side of the foot of Mt. Hakken-zan and late April to early May in Tsuneji-zawa and Bankei. The founding queens appear in late April probably about two or three weeks after the disappearance of the snow cover. The nest is started in early May in Hakken-zan and in late May in Tsuneji-zawa and Bankei. No detailed observation was made on the behavior in the post-hibernant stage, lasting about 2~3 weeks since the departures from hibernacula to the start of nest construction. But the meager data indicate no particular difference between two species concerning this stage.

According to Yoshikawa (1962 a), the post-hibernant stage in *jadwigae* begins in middle March, lasting about four weeks until middle April in Osaka. Delayed appearance of founding queens and short post-hibernant stage are remarkable in Sapporo, apparently caused by severe climatic conditions as given in Fig. 9. Shortening of post-hibernant stage is also noteworthy, which could be regarded as a compensation for the delayed spring appearance.

### 2.2. Solitary stage

2.2.1. *Presence of pleometrotic nest foundation in snelleni*: As in most polistine wasps studied in temperate zone (Morimoto, 1953 b, Yoshikawa, 1962 c), the nest foundation by a single female, that is, haplometrotic foundation, is prevailing both in *snelleni* and *biglumis*. In *biglumis*, the writer confirmed no foundation by more than one female or pleometrotic foundation among about 10 cases observed. In *snelleni*, too, all of more than 100 cases observed were haplometrotic except for the single instance as described here.

This nest (No. 6808) was observed at Mt. Hakken-zan from May 26 to July 7, 1968. Two queens shared one nest made under rock overhang. It is unknown either they lived together since the start of the nest or one of them joined after the nest was founded by the other. Unfortunately, the nest was unsuccessful. Both females disappeared successively in early July resulting in the evacuation of the nest. The writer could not confirm any cooperation or definite dominance order

between them throughout the period, though no detailed observation was undertaken. This case may be regarded as an unsuccessful instance of the temporary pleometrosis in terminology by Yoshikawa (1962 c), that is, the coexistence of two or more queens in the early stage without cooperating for nest development, followed by their dispersion leaving one queen. Yoshikawa (1957) recorded a similar case in *jadwigae*, and Rau (1940) also reported the commonness of the pleometrotic foundation in *annularis*.

In *gallicus*, it is well known that pleometrosis is rare in central Europe, while frequently observed in Italy (Pardi, 1942). The occurrence of nest foundation by this method in Sapporo, standing near the northern limit of the north temperate zone, is seemingly very exceptional.

2.2.2. *Rate of cell construction:* A clear difference exists between *snelleni* and *biglumis* concerning the construction rate, that is, the number of cells constructed per day.

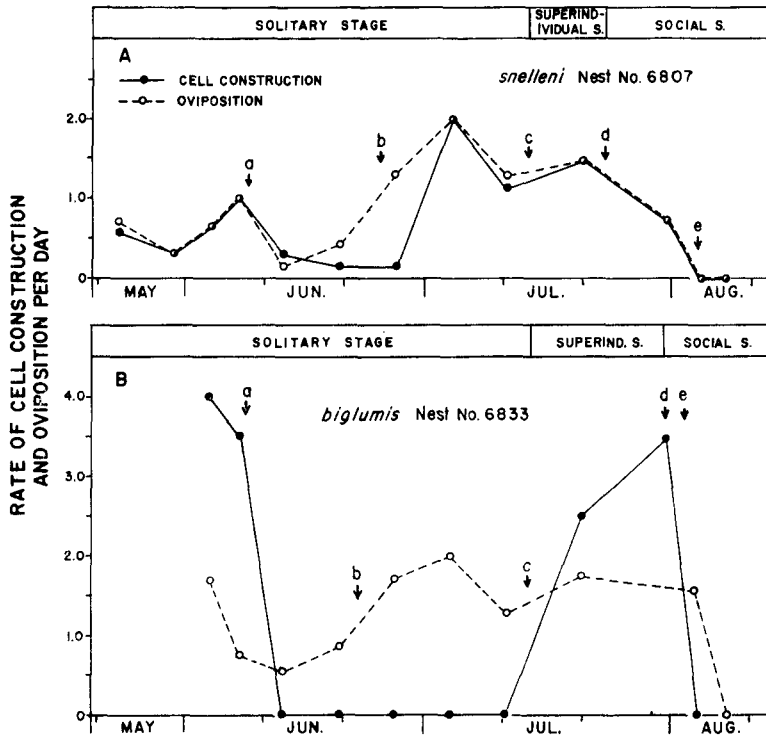


Fig. 3. Changes in rates of cell construction and oviposition in representative nests of *snelleni* and *biglumis*. a. Hatching of new larvae, b. Cocoon spinning, c~e. Emergence of workers, males, and young queens.

In *snelleni*, the construction rate is at first relatively high. Then, the rate drops conspicuously after the hatching of larvae. But construction is never stopped completely, continued slowly until the later reactivation (Fig. 3, A.) This reactivation seems to have an intimate relation to the maturation of larvae or the cocoon spinning. In some nests the highest construction rate is obtained before the emergence of workers. In others, however, the rate continuously increases until the first worker emerges. The pattern of nest development in the solitary stage in *snelleni* shows, therefore, a relatively mild and monotonous increase with a very shallow concavity (Fig. 4).

Consequently, the number of cells constructed before the hatching of larvae is rather smaller than that in the period from the hatching of larvae to the emergence of the first worker. In Nest No. 6807, for instance, the founding queen constructed 18 cells before the hatching of larvae, 10 cells from that time to the cocoon spinning by larvae, and 24 cells after the spinning to the emergence of workers. Therefore, only 35% of total cells completed by the founding queen was made before the hatching of larvae, and about the half after cocoon spinning. The number of cells constructed per day in the average of every seven days' count was usually less than 2.0 in Nest No. 6807.

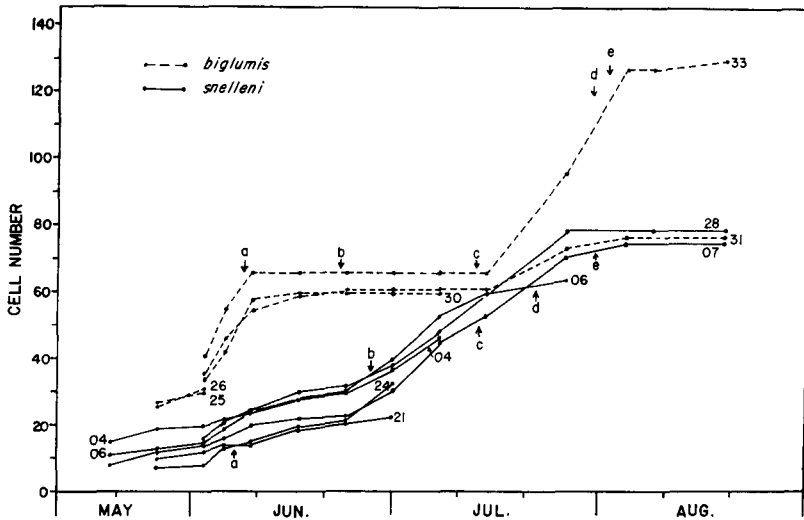


Fig. 4. Increase of the cell number. a~e (cf. Fig. 3).

In contrast to *snelleni*, cell construction is completely stopped in *biglumis* after the hatching of larvae (Fig. 3, B). This fact agrees to the observations on *chinensis* by Morimoto (1954 b) and Yoshikawa (1962 a). Moreover, the construction rate does not recover even after the maturation of larvae or cocoon spinning. Even if the queen makes cells in this inactive period, the number does not exceed



Table 1. Number of cells constructed and cocoons produced in solitary stage in certain selected nests

Nest No.	A. cells constructed in solitary stage	B. Cells constructed throughout season	A/B (%)	Cocoons produced in solitary stage
<i>snelleni</i>				
6804	47	—	—	9
6806	55	(64)*	(85.9)	10
6807	47	75	62.8	6
6808	37	—	—	12
6818	26	—	—	—
6828	49	78	62.9	9
6832	34	—	—	6
6840	51	(57)*	(89.5)	12
6841	26	—	—	1
<i>biglumis</i>				
6830	60	—	—	8
6831	61	(77)*	(79.3)	12
6833	66	130	50.8	8

Except for B, the figures are given based upon the last observations before the emergence of workers. Therefore the real figures for solitary stage must be slightly higher.

\*: Destroyed just after the emergence of workers. The real figures must be larger than those indicated.

0.5. Thus, the curve of the increase of the cell number shows a distinct plateau after the emergence of larvae (Fig. 4). More than 90% of cells prepared by the founding queen are completed in the period before the hatching of larvae.

The number of cells produced by a single queen in the solitary stage reaches 40 to 55 in successful nests of *snelleni* and about 60 in *biglumis* (Tab. 1). The percentages of the cells made by the founding queen to total cells produced until disintegration of colonies are estimated about 70% in *snelleni* and 50% in *biglumis*, distinctly higher than in *snelleni* and *chinensis* in southern Japan, where 30~40 cells, that is about 15% of the total production, are completed by a founding queen (Morimoto, 1954 a and personal communication, Yoshikawa, 1962 a).

Deleurance (1957) divided construction activities into three categories, construction of petiole, that of new cells, and elongation of cell walls. In the present observation, too, such differentiation was distinguished in both species. The cell walls were elongated irrespective of new cell construction, in parallel to the growth of the larvae even in inactive period after the hatching of larvae.

2.2.3. *Changes in oviposition rate:* In *snelleni* (Nest No. 6807), the rates of oviposition and cell construction show a marked synchronism throughout the solitary stage (Fig. 3, A). Trend of oviposition rate is therefore similar to that of cell construction rate. The oviposition rate reduces by the hatching of larvae, but increases after the cocoon spinning by old larvae. In no nest the oviposition stopped completely after the hatching of larvae. Two peaks of oviposition rate

are observed, in this stage, one at or near the hatching of larvae and, the other, the higher, slightly before the emergence of the first worker. Apparently the recovery of oviposition rate is intimately correlated to the cocoon spinning by old larvae.

Number of eggs laid per day per queen is usually less than 1.5 in average of each seven days' count. In no average case the queen laid more than two eggs per day. The construction of a new cell is not always followed by the immediate oviposition into it. On the other hand, the queen sometimes lays two eggs in one and the same cell in spite of the presence of vacant cells. In such case only one egg develops to be adult.

In *biglumis* (Nest No. 6833), too, two peaks of oviposition rate are found, one before the hatching of larvae and the other, after the cocoon spinning, as in *snelleni*. But in contrast to the latter, *biglumis* is characterized by the absence of parallelism between rates of cell construction and oviposition (Fig. 3, B). The oviposition rate was 1.7, before the hatching of larvae, dropped to 0.5 parallel to the complete cessation of cell construction after the hatching of larvae. The cocoon spinning by old larvae seems to cause the recovery of oviposition as in *snelleni*. The oviposition rate increased to 2.0 just before the emergence of the worker. But this raise is not followed by the cell construction, giving a clear difference from *snelleni*.

The cessation of oviposition after the hatching of larvae was observed in the other two nests of *biglumis*. In Nest No. 6831, the oviposition stopped after the hatching of larvae, and recovered after pupation: The highest oviposition rate 3.7 in average, was obtained about 10 days before the emergence of workers. Thereafter the oviposition rate decreased without recovery even after the emergence of workers. The subsequent fate was not followed because the nest was partly destroyed by either birds or rodents at the emergence of workers so that only a few workers and young queens were produced. The fluctuation of the oviposition rate mentioned above approximately corresponds to the observations with the southern population of *chinensis* by Morimoto (1954 b).

Probably the trend mentioned above is common to the species in the north temperate zone. The decreased oviposition after hatching of larvae and its recovery after cocoon spinning obviously correlate to the amount of foraging activities by the founding queen.

*2.2.4. Brood population trend:* Population trends in two representative nests, Nos. 6807 (*snelleni*) and 6833 (*biglumis*) are shown in Figs. 5 and 6, where the number of individuals in successive immature stages is given together with the number of empty cells. In later phases of colony development, especially after the successive emergence of workers, the increased hostility sometimes made exact counts of various stages difficult. In such instances, as expressed in Fig. 5, with dotted lines, actual counts were replaced by estimates with the observation errors of about  $\pm 5$ . The maximum of the total brood is attained in late July in

*snelleni* and in early August in *biglumis*, followed by a decrease due to emergences of a large number of adult.

Eggs laid toward the end of colony cannot give adults, died or eaten by adults in egg or larval stages. In *snelleni*, both eggs and larvae disappear in middle and later August respectively. In *biglumis*, however, eggs disappear in middle August, but larvae remain till later September. These last larvae are poorly fed perhaps by young queens, but cannot grow to adults due to poor nutritional and thermal conditions. The last young queens emerge in middle September in both species.

In both species, the number of cocoons produced within the solitary stage is about 10 in normal colonies (Tab. 1), occasionally more than 12 being slightly higher than in *chinensis* (Morimoto, 1954 a). No significant difference in brood population trend was detected between two species, except for the later survival of larvae in *biglumis*. The specific difference in the number of empty cells in the solitary stage will be mentioned in the next section.

2.2.5. *Number of empty cells:* As the queen of *snelleni* lays eggs in parallel to the construction of cells (cf. Section 2.2.3.), the number of empty cells is always small throughout the solitary period rarely exceeding 20% of the total number (Fig. 2, A and 5), and about 90% of cells, sometimes all, are occupied by broods. Thereafter, the empty cells increase caused by the decreased oviposition activity and the specific habit that the queen does not reuse cells once occupied by brood.

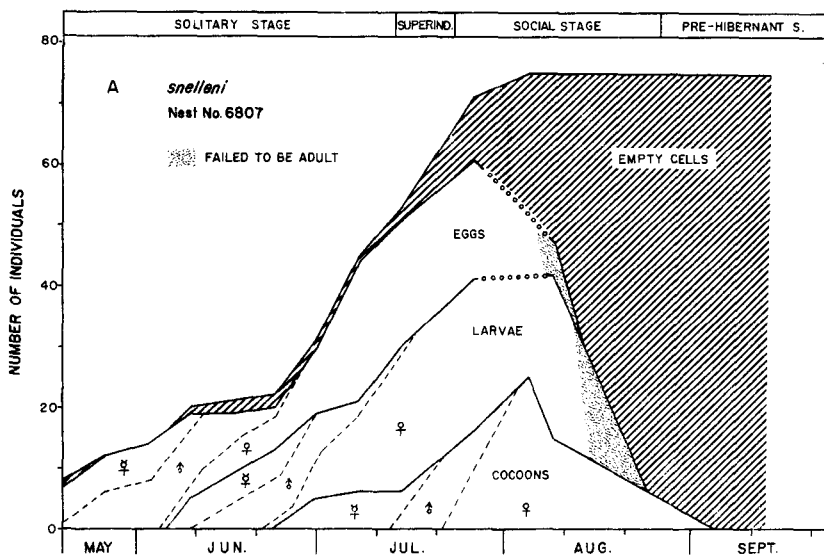


Fig. 5. Brood population trend in representative nest of *snelleni*. Individuals of each immature stages are divided into three castes.

Rapid increase is observed from early August resulted from an intensified emergence and decrease of brood.

In *biglumis*, eggs are laid only in cells situated at the central and upper parts in the early solitary stage, never in those at the lower and peripheral parts (Fig. 2, E). In early nests, empty cells occupy more than 50% of total cells (Fig. 6), then decreases by the reactivation of the oviposition, for instance, in Nest No. 6833, reaching the minimum, 14% of total cells. Thereafter, empty cells again increase because the rate of cell construction by successively emerged workers exceeds the

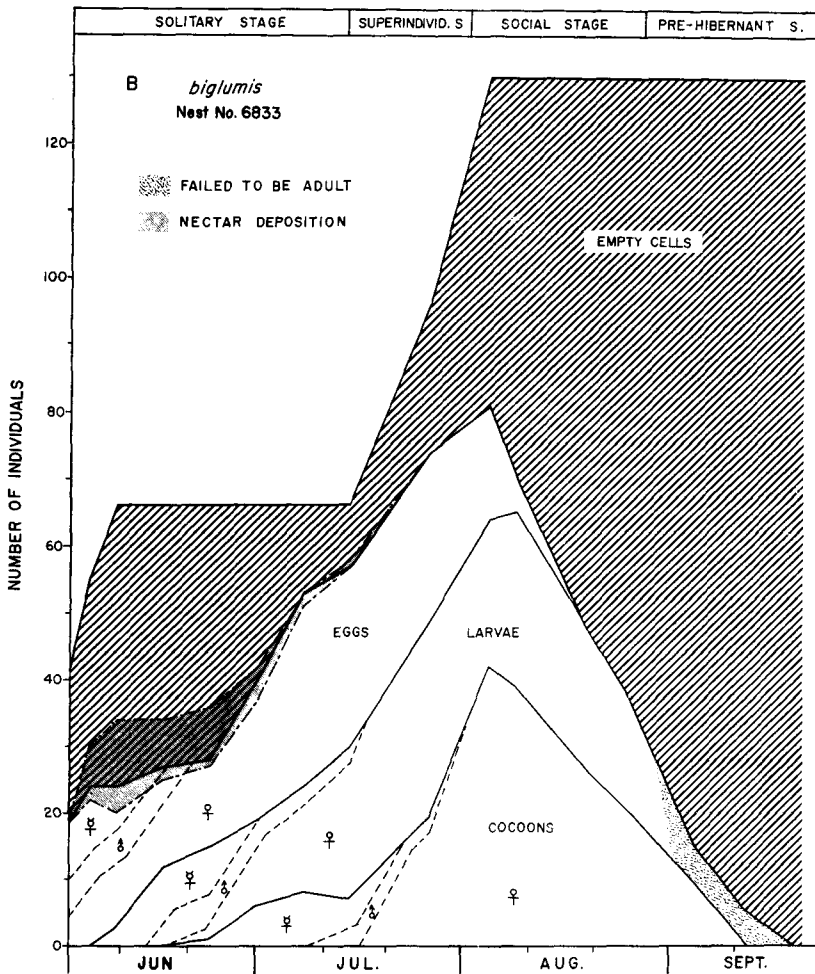


Fig. 6. Brood population trend in representative nest of *biglumis*. Individuals of each immature stages are divided into three castes.

rate of oviposition by the queen. After middle August, increase of empty cells is accelerated by the cessation of oviposition and emergence of young adults.

2.2.6. *Nectar storage in biglumis*: Morimoto (1959) reported that the founding queen of *chinensis* stored nectar drops in cells during the solitary stage, especially at the hatching of new larvae. On May 26, two nests of *biglumis* with such nectar storage in several cells were discovered at the foot of Mt. Hakken-zan, both with about 30 cells and 10 eggs. The same condition was seen on June 2, but these nests were abandoned by the founding queens after the transplantation into the writer's garden. Three other nests with nectar deposition were discovered at the same area. In one nest, No. 6833, with 55 cells and 24 eggs, nectar storage was confirmed on June 5 in eight cells situated at the lower part of the nest. The founding queen of this nest began to collect eagerly nectar drops for several days before hatching of larvae. Both number and volume of each nectar drops stored in the cells reached the maximum just or slightly after the hatching of new larvae (Fig. 6). Both number and size of stored drops decreased with cocoon spinning, though remained in a small number even after emergence of workers. In each cell, at first one droplet or more appear. Then, these droplets fuse one another and the amount increases gradually. Consequently the real amount of nectar storage at the hatching of larvae is larger than that shown in Fig. 6 by the number of cells. As mentioned above, founding queens always store nectar in drops in the cells situated at the lower part of the nest, where eggs are usually not laid down. Even if the nectar is occasionally laid in the cell with an egg, it is removed at the hatching of the larvae.

In spite of the number of nests observed higher than in *biglumis*, such nectar storage was observed in few nests of *snelleni*. Even if deposited, the number and size of droplets were far inferior than in *biglumis*, suggesting a probable specific difference.

### 2.3. Superindividual stage

Superindividual stage is defined as the period during which the founding queen and newly emerged workers coexist and cooperate for the maintenance of the colony (Yoshikawa, 1959, 1962 b). In Sapporo this stage lasts for only one or two weeks, from the emergence of the first worker to that of the first male. This short duration and the small number of workers produced give sharp contrast to the polistine populations in southern Japan.

2.3.1. *Emergence of workers*: The workers emerge in and near Sapporo from early to late July, about half to one month later than *jadwigae* in Osaka (Yoshikawa, 1962 b). The dates of emergence of the first worker are greatly affected by the environmental conditions. The first worker of *snelleni* emerged in early to middle July in 1968, at the foot of Mt. Hakken-zan, about a week later in Tsuneji-zawa in 1962. The first worker of *biglumis* emerged in middle July in Hakken-zan in 1968, without marked difference from *snelleni* in the same area. In both species all workers emerge successively within several days. They are produced from eggs laid down at the beginning of the nest foundation. The total incubation

Table 2. Number of adults produced and productivity

Nest No.	A. Total cells produced	B. Total eggs laid	C. Total emergence	C/A (%)
<i>snelleni</i>				
6217	87	85	65	74.8
6225	66	—	46	68.1
6807	75	74	54	66.8
6828	78	82	50	64.1
6842	47	—	22	46.8
6844	98	—	75	76.5
<i>bighemis</i>				
6831	78	75	15	19.2
6833	130	117	86	66.1
6850	114	—	57	50.0
6851	102	—	37	36.7
6852	109	—	37	33.9
6853	91	—	22	24.2
6854	62	—	11	17.8
6855	101	—	49	48.5
*6860	70	—	28	40.0
*6861	152	—	69	45.4

Except for the number of total cells produced, the figures give the estimates, because of brood loss which was not checked. \*: Taken at Oketo. ♀: Dwarf queen

period of the worker is about 60 days, divided into egg stage 25 days, feeding larval stage 15 days, and postfeeding larval and pupal stage 20 days.

The number of total workers produced is about 5~15 (Tab. 2), estimated on the basis of the count of the number of individuals on the nest and cells which became empty after emergence leaving cocoons. At any rate, the small number of workers is remarkable in comparison with the populations in southern Japan.

*2.3.2. Duration of superindividual stage:* The duration of this stage is extremely short ranging from only a few days to near three weeks, in average about a week. Yoshikawa (1962 b) reported that the superindividual stage lasts for two months in *jadwigae* in Osaka, about 1.5 months longer than in Sapporo. Short period and small number of workers must affect the social organization of *Polistes* in the northern part of the north temperate zones. Although no ethological and functional analyses were made in this preliminary study, the writer assumed that the superindividual organization, one of the most characteristic features in social insects, is greatly reduced in the polistine wasps in this region.

*2.3.3. Cell construction:* The third peak of cell construction in *snelleni* (Nest No. 6807) was obtained just after the emergence of workers (Fig. 3, A). Number of cells completed in this stage is about 10, occupying only about 15% of the total cells. The construction is made mainly by workers, but newly emerged workers rest on the nest for a few days neither foraging nor making any

in certain selected nests

C/B (%)	♂	♂	♀	♀	No. of reused cells (Adults produced)
76.5	14	12	40	0	0
—	11	12	23	0	0
73.0	7	13	29	5	0
61.0	6	16	30	—	0
—	5	10	7	—	0
—	> 2	15	45	0	0
20.0	4	0	8	3	2 ( 2)
73.5	8	10	50	3	14 (11)
—	2	10	—	—	—
—	—	7	16	1	—
—	—	11	10	6	2 ( 2)
—	2	4	6	—	—
—	—	—	—	2	—
—	1	6	24	3	7 ( 5)
—	—	—	—	—	—
—	—	—	—	1	—

with observation errors of about  $\pm 5$ . Number of total eggs may be slightly higher, with small body size as workers.

other tasks. In this earlier period, nest construction is still made by the founding queen. However, the third peak is probably due to workers, but even then the queen occasionally joins to this work.

In *biglumis* (Nest No. 6833), the cell construction began again after the emergence of workers (Fig. 3, B). A rapid expansion of the nest seemingly mainly performed by workers, was seen till the end of July when males and new queen emerged. Number of cells constructed in this stage, lasting for about 20 days, mainly by workers, reached about 70, that is, more than the half of total cells produced. The rate of construction was 3.5 cells per day in nine days' average at the peak of the activity in the later part of this stage.

**2.3.4. Oviposition by the founding queen:** Both nests in Fig. 3 show the third peak of oviposition rate just after the emergence of workers, but this final peak does not always appear. In this stage, as in the later part of the solitary stage, the founding queen of *snelleni* lays eggs only in newly constructed shallow cells, never in those which became empty after the emergence of occupants. Consequently most cells are used only once during the season (Tab. 2 and Fig. 2, C). When the queen rarely lays eggs in cells once used, they cannot give adults, either died or eaten by adults before pupation. Since larvae normally occupy newly made cells, no enough food may be supplied to those abnormally reared in old cells remote from the larval area.

On the contrary, the founding queen of *biglumis* lays eggs in any empty cells occupying the central part of the nest. She does not lay eggs in cells situated at the nest margin, even if they are regularly constructed in shape. She also does not lay eggs in irregularly shaped cells constructed at the nest margins in later part of this period. In Nest No. 6833, for instance, 86 out of 130 cells, or 66%, were used for brood rearing, but the other ones, 37 were never used. The number of cells used twice were 14, or 11% of total cells, and eleven of them produced adults (Tab. 2 and Fig. 2, G.)

#### 2.4. Social stage

The social stage is defined as the period between the emergence of the first male to the death of the last worker (Yoshikawa, 1959, 1962 a, and 1963 a, and b). No remarkable expansion of the nest can be seen in this stage.

*2.4.1. The production of males and young queens:* Within the limit of the available information, males of *snelleni* emerge after the emergence of all workers, in Hakken-zan from middle to late July. The duration spent for the emergence of all males is one or two weeks. The cells producing male form a cluster separated from those producing workers. *Biglumis* males also emerge from late July in the same area, some of them within a period of one or two weeks in late July, but some others toward the end of colony development. These males emerge from the eggs laid in the cluster of cells for young queens, seemingly by either accidental haploidy or the oviposition by workers (Spradbery, 1965). The first young queen of both species emerge from late July to early August, about a month before the colony disintegration in Hakken-zan. The early part of them frequently overlaps with that of males. The fact that the brood reared in the spring solitary stage involves some males and young queens seems to be one of the peculiar features in the northern part of north temperate zone, because these reproductives are mostly produced in the superindividual stage in the southern populations.

*2.4.2. Dwarf queens in late colonies:* Toward the end of the colony, both species frequently produce some dwarf "queens". Certain problems concerned are as follows: 1. How the body size decreases toward the end of colony? 2. Whether they have chances to mate with males or not? 3. Whether they can hibernate, survive to the next year and found new nests? 4. What is their social status?

These dwarf queens, emerging in late August to middle September in *snelleni* and in late August to early October in *biglumis*, are produced from eggs laid by the final oviposition activity by the founding queen in early August. At this time only a few workers remain so that a severe food shortage is likely to occur. The larvae in middle August are indeed small for their age than these in earlier periods, suggesting the poor nutritional conditions. It is plausible that they cannot attain the normal body size because of such food deficiency. When the last females emerge, most males are already dead so that the chance of mating



is hardly to occur. Moreover, it is probable that they cannot survive until the next spring because of their inferior physiological conditions. Virtually such dwarf queens are seldom seen in spring.

Young queens are distinguished from workers by larger body size and inactive behavior. In both species concerned, young queens with normal body size are always larger than the workers. But their body size gradually decreases toward the end of the colony. Intermediate forms are produced and even individuals smaller than the normal worker appear. If the body size is adopted as the unique criterion to separate castes, a few extremely small females must be classified into workers. But in the present case, dwarf queens show the inactive desposition characteristic to normal queens and the cause of the decreased body size is fairly certain. Consequently, these individuals must not be regarded workers, simply representing the malformed queens.

*2.4.3. The number of males and young queens produced:* As already explained in case of workers, exact numbers of males and young queens produced could not be counted in the present study, but approximate estimates are given in Tab. 2. The number of males produced by *snelleni* per nest ranges 10~20 in successful colonies, less than 10 in small colony with about 50 cells. These figures are comparable to or slightly higher than the number of workers produced. The absence of male production was not confirmed among more than 100 nests observed in *snelleni*. Successful colonies of *biglumis* produced the males the number of which is comparable to that in *snelleni*. One out of nine nests produced no males.

The production of young queen depends greatly upon the colony size, ranging 30~50 in normal colonies of *snelleni*. In 1962 the writer observed the production of about 100 young queens in a strong *snelleni* nest with 140 cells. On the other hand, the poor colonies produce only several queens. In *biglumis* the queen production is slightly inferior than in *snelleni*. At any rate the numbers of effective founding queens must be less than those mentioned in Tab. 2.

Total adults produced depend upon the colony size, usually less than 100 with no marked difference between two species. Total adults produced per total cells range 45~80% in *snelleni* and 20~70% in *biglumis* (Tab. 2). On the other hand, the both species in and near Sapporo are characterized by the higher percentage of reproductives produced compared with workers. In normal colonies, the percentage ratio of the workers produced is less than 25%, while young queens occupy more than 50%. The scarceness of workers is also reproted by Deleurance (1957) in his experimental indoor breeding of *gallicus*, where the workers occupy only 0.6% of the total population. Yoshikawa (1963, b), in contrast to the present observation, reported that the ratio of the worker, male, and young queen as 8:1:1 in *jadwigae*.

*2.4.4. Behavior of male and young queen:* Descriptions given here include partly the behavior in pre-hibernant stage until the colony disintegration. Males of both species usually rest attaching around the nest, beg food from workers and

occasionally depart from the nest. The homing to the nest was confirmed by five males of *snelleni* marked with yellow paint, all of which returned to the nest within 30 minutes after the liberation at about 5 m apart from the nest. Flower visits by males are often observed in this period even before the deaths of workers, implying the food intake by themselves. They never bring back meat balls or nest materials, but the writer once observed in Nest No. 6217 (*snelleni*) in 1962, that one male received a meat ball from a worker, malaxated it and then gave it to larvae. Such rudimentary parental care is very rare but is also recorded in *Vespa lewisii* (Shida, 1954).

In *snelleni*, most young queens rest on the surfaces of the nest avoiding direct insolation. In *biglumis*, some young queens behave similarly, but many of them insert the bodies deeply into cells, exposing only the tips of metasomata. Inactivity is the principal disposition in young queen of both species, but they rarely go out to take food for brood and themselves. Furthermore, they bring water drops and ventilate the nest on hot days. Food regurgitation among them is also observed. These items of behavior are seen even in the presence of workers. Although keeping usually their inactive resting on the nest, the young queens of *snelleni* show occasionally an aggressive behavior to the observer when he approaches the nest. Such attack by young queens is not seen in *biglumis* and so far is unknown in any polistine species. The question arises that such aggressive individuals in *snelleni* might be virtually large workers. Such possibility is not excluded in southern populations with many quite large workers. In the present case, however, females making such attacks are certainly the young queens for their characteristic desposition.

### 2.5. *Pre-hibernant and hibernant stage*

Only young queens survive three extranidal stages, pre-hibernant, hibernant and post-hibernant. The last stage was already referred to. Here the other two stages are briefly described.

2.5.1. *Pre-hibernant stage*: Yoshikawa (1959, 1963 b) defined the pre-hibernant stage as the period from the death of the last worker to the migration of young queens into hibernacula. In and near Sapporo, this stage lasts for about five weeks, from late August to late September. In both species, founding queens die in early to middle August. Of four successful colonies in Hakken-zan area, two *snelleni* and two *biglumis* ones, one colony of each species lost the founding queen in early August, the other two in middle August. All workers and one of these nests disappeared in late August. Six nests of *biglumis* and one nest of *snelleni* discovered in Hoheikyo lost the founding queen and most workers when inspected on August 20, 1968. Workers in the fall are distinguished from dwarf young queens by heavily worn wings. Even after the death of workers, the colonies are inhabited by males and young queens, the behavior of which was already described briefly in the preceding sections.

The active phase of the life cycle ends by the disintegration of the colony.

The disintegration ordinarily takes place from late August to middle September, though colonies of *biglumis* tend to persist later than *snelleni*. Not all males and young queens in colony synchronously leave the nest, often gradually since middle August.

In *biglumis*, near or after the disintegration, some already dispersed males and young queens fly around the nest without returning to it. This phenomenon is observed to the early October, especially on fine days. It is likely that mating is done in this way, though no direct observation was made. In *snelleni* such flight around the nest is scarcely seen after the disintegration. Probably they go directly to hibernacula.

2.5.2. *Hibernant stage*: This is the longest stage in the annual cycle of northern *Polistes*, lasting nearly seven months until late April of the next year. The hibernacula of both species in and near Sapporo are still unknown. In other species, the following places are reported: Crevices of rocks, *annularis* (Rau, 1942), vacancies under roof tiles and above the ceiling, *chinensis* and *jadwigae* (Yoshikawa, 1963 b), rotting woods and barks of dead trees, North American *Polistes* (Michener and Michener, 1951), rotting woods and under the surface of the ground, *Vespa* and *Vespula* in Hokkaido (the writer's observation) and South Japan (Matsuura, 1966).

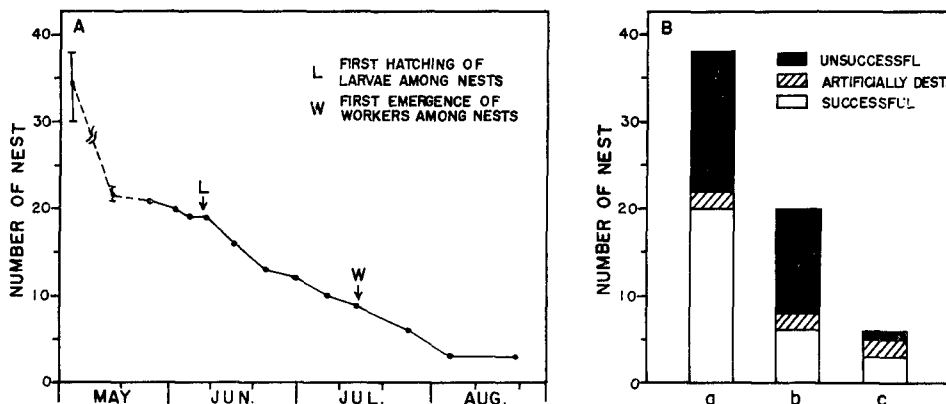


Fig. 7. A. Change of the number of *snelleni* nests throughout seasons at Hakken-zan. B. Survival ratio of *snelleni* nests in each developmental stage. a. Before hatching of larvae. b. From hatching of larvae to emergence of workers. c. After emergence of workers.

### 3. Evacuation and survival of nests

Up to the present, the descriptions were given mainly based upon the observations made with successful nests. As is given in the introduction, only three out of 38 nest in *snelleni* and two of five in *biglumis* continued until the end of the season in nest aggregation at Hakken-zan. Here some observations on the evacuation and survival of nests are referred to, which are suggestive to the

preparation of ecological life tables of *Polistes* wasps in future.

Records of these unsuccessful nests in *snelleni* are shown in Figure 7 and Table 3. The causes of nest abandonment are variable such as evacuation (Yoshikawa 1962, a), attacks by natural enemies, and human interference. Except for those removed by artifacts (two to 5%), 42% of total nests most of which possessed less than 10 cells, ceased their development before the hatching of new larvae, mainly by the evacuation by the founding queens. The highest rate of cessation, 70% of survived nests, was obtained in the period from the hatching of larvae to the emergence of workers, suggesting that the presence of larvae and cocoons did not inhibit the evacuation, and probably released attacks by natural enemies. Only six nests produced adults but one of them was destroyed just after the emergence of workers by some unknown accidents in late July. In each period, two nest were lost by some human interference. If these destroyed after the emergence of workers and reproductives are regarded successful, the survival ratio becomes 83% in that period. Consequently the first critical period is just at the beginning of the nest foundation and the second one at the period between hatching of larvae to emergence of workers. At any rate, 82% of total nests were extinguished during the solitary stage. This fact seems to support the ascertainment by Yoshikawa (1962 a), who regards the solitary stage as a critical period in polistine life cycle. However, it must not be ignored that this stage is very long in northern Japan compared with the later stages, so that the chance of nest cessation is higher even purely statistically.

Some data on nest survival on *biglumis* are added to. At Hoheikyo one nest group of *biglumis* consisted, on August 20, 1968, of one successful nest and four others perhaps evacuated in spring, each with about 30 cells. Another group at the same area was very successful, with five nests closely standing one another, when observed on the same day. No abandoned nest was detected nearby. At Hakken-zan two of five nests were destroyed by the human interference at the start of nest foundation, another one just before the emergence of workers, and the other two continued to the production of reproductives as repeatedly referred to in the preceding sections (Nos. 6831 and 6833).

For the time being, it is difficult to find a significant relation between survival and density. Among five successful nests, four (Nos. 6806, 6807, 6828, and 6841 in Fig. 8) belonged to the largest group, consisting of 14 nests and the other, No. 6840 was found remote from other groups. Apparently the evacuation by the founding queen plays an important role for the realization of such low survival. The evacuation may sometimes be caused by ecological factors, but it is possible some physiological maladjustment is responsible in many instances, which requires further analyses. The survival in this group of *snelleni* is very low. But this is not characteristic to the species. Though not precisely studied, the survival ratio was higher in other instances.

Some eggs or larvae were lost in most nests of the both species. The rate of loss to total brood was within 20% usually 5~6% all in *snelleni* before nest

extermination. Three exceptions are as follows: Nest No. 6808 in which temporary pleometrosis was seen (*cf.* 2.2.1.), lost many young just before the dispersion of the two queens. In No. 6818, the comb surface was exposed to direct insolation by the translocation of the nesting substratum. This caused the loss of more than 40% of total brood. Finally No. 6832, constructed at shade place, lost 27% of total brood before extermination.

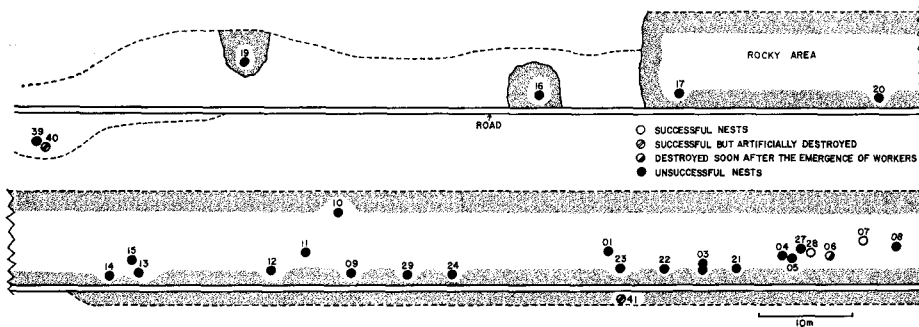


Fig. 8. Spatial distribution of *snelleni* nests at the foot of Mt. Hakken-zan.

The ratio of brood loss in successful nests of both species ranged 20~40% of total eggs laid throughout the seasons (Tab. 2), especially towards the end of colony. For instance, No. 6807 (*snelleni*) lost one egg and two larvae in the solitary stage but more than 13 young after the emergence of the worker, and No. 6833 (*biglumis*) lost eight eggs and one larva in the solitary stage while 18 young after the emergence of workers. Egg eating behavior by the founding queen was reported in some species (*gallicus*, Deleurance, 1957; *chinensis*, Motimoto, 1954 a). In the present case the loss of eggs in the solitary stage was perhaps caused by such behavior. The frequency of oophagy may be higher than supposed because of the oviposition often takes place immediately after oophagy.

### Concluding Remarks

#### 1. Specific ethological differences between *snelleni* and *biglumis*

No marked deviation exists between *snelleni* and *biglumis* concerning the general pattern of the life system, but some differences, presumably of species-specific, are recognized, as summarized below: 1. Nest site selection (*cf.* section 1. Further observations are required). 2. Cell construction by the founding queen (*cf.* 2.2.2. Synchronized with oviposition in *snelleni*, not in *biglumis*). 3. Oviposition by the founding queen (*cf.* 2.2.3. Laid in most cells in *snelleni*, only in the central part of the nest in *biglumis*). 4. Nectar deposition (*cf.* 2.2.6. Observed in *biglumis*, not in *snelleni*). 5. Reuse of brood cell (*cf.* 2.2.4. Observed in *biglumis*, not in *snelleni*). 6. Male production (*cf.* 2.4.1. All emerging in late July in *snelleni*,

Table 3. Records of unsuccessful nests

Nest No.	Date of last observation	Observation period	Total cells produced	Eggs
*6802	May 19	1	12	—
*6803	"	1	10	—
6805	"	1	8	7
*6809	"	1	8	—
*6811	"	1	12	—
*6813	"	1	9	—
*6814	"	1	10	—
*6815	"	1	3	—
*6816	May 26	1	4	—
*6817	"	1	0	0
*6819	"	1	10	—
*6820	"	1	0	0
*6822	"	1	0	0
*6823	"	1	1	—
*6827	"	1	0	0
*6829	"	1	0	0
*6856	"	1	1	—
6801	Jun. 9	15	29	17
6812	"	8	18	17
6834	"	1	27	15
6838	"	1	21	20
6839	"	1	22	12
6810	Jun. 16	22	24	15
6835	"	8	25	11
6821	Jun. 21	29	23	13
6824	Jun. 30	36	33	12
6804	Jul. 7	49	47	22
6808	"	49	37	22
6818	Jul. 14	49	26	6
6806	Jul. 26	68	64	12
6832	"	61	34	20

Number of total brood is expected slightly higher than the figures indicated, because  
 \*: Already destroyed or evacuated before the discovery.

some of them emerging toward the end of the colony in *biglumis*). 7. Ratio of total adults produced to number of total cells produced (cf. 2.4.3. Higher in *snelleni* than in *biglumis*). 8. Aggressive behavior by young queens (cf. 2.4.4. Observed in *snelleni*, not in *biglumis*).

Since these differences were already described in the preceding sections, here the writer would like to give some remarks only to one aspect, the relationship between oviposition and cell construction by the founding queen.

Studying this relation in *gallicus*, Deleurance (1957) came to the conclusion that the cell construction was restarted by the founding queen only when all so far

in *snelleni* at last observation

Brood		Lost of brood throughout observation period		Total brood
Larvae	Cocoons	Eggs	Larvae	
0	0	—	0	—
0	0	—	0	—
0	0	—	0	7
0	0	—	0	—
0	0	—	0	—
0	0	—	0	—
0	0	—	0	—
0	0	—	0	—
0	0	—	0	—
0	0	0	0	0
0	0	—	0	—
0	0	0	0	0
0	0	0	0	0
0	0	—	0	—
0	0	0	0	0
0	0	0	0	0
0	0	—	0	—
9	0	1	0	26
0	0	0	0	18
10	0	—	—	25
0	0	—	—	20
10	0	—	—	22
6	0	0	4	25
13	0	0	0	24
8	0	4	2	27
10	4	1	2	29
15	9	1	1	48
3	12	9	16	52
15	2	6	10	39
29	11	1	2	65
4	6	10	1	41

unchecked additional loss of brood is possible.

made cells are occupied by eggs. Further he postulated that the construction was controlled by the innate system like as in many solitary wasps (Iwata, 1942). On the other hand, Morimoto (1954 c) recorded no such definite correlation between oviposition and the presence of empty cells in *chinensis*, suggesting that oviposition is not inevitably conditioned by the increase of empty cells. The presence of a correlation between these two items in *snelleni* favors the opinion by Deleuranee. But the fact that nests usually have a few empty cells suggests that such correlation is not so strict as in *gallicus*. Moreover, the ample presence of empty cells in early *biglumis* nest does not support his theory. The liberation from a stereotypic

chain sequence of a series of performance is regarded one of the important elements in the social evolution in insects (Weyrauch, 1939). In higher ants (Otto, 1958) and honeybee (Sekiguchi and Sakagami, 1967) workers can start and end most tasks from and at any steps of a chain sequence. The transition from stereotypic chain sequence to the liberation is known even in the nesting habit of certain halictine bees (Sakagami and Michener, 1962). It is not impossible that diverse species of polistine wasps show various steps of such transition. The large number of species involved in this genus with nearly cosmopolitan distribution may favor the extensive comparative studies on this aspect, together with intensive analyses with selected species both in solitary and later stages of the annual cycle.

## 2. Comparison of life cycle between northern and southern population in Japan

Although the sequence of various stages given in preceding sections shows no essential difference between *snelleni* and *biglumis*, it might not always be adequate to present the life cycle pattern based upon the observation of these two species because *snelleni* is a temperate species while *biglumis* is distributed in cool temperate to subarctic zone in the Northern Hemisphere. Therefore, the life cycle pattern of *snelleni* in and near Sapporo is tentatively compared with that of *jadwigae*, a representative southern species in Japan (Fig. 9). Based upon this comparison, the writer would like to give some preliminary considerations upon the differences of life cycle between northern and southern Japan in relation to environmental conditions. Most important characteristics of the life cycle in northern Japan are enumerated as follows: 1. Active period lasting from nest foundation to colony disintegration is short apparently affected by severe climatic conditions. 2. Two extranidal stages and superindividual stage are especially shortened. 3. Number of produced workers decreases especially in comparison with that of reproductives. 4. Production of reproductives begins already in the early part of the solitary stage. 5. Many, if not most, parts of the work for maintenance and development of colonies are performed by the founding queen.

Apparently severe climate is one of the most important factors for the realization of such life cycle. The severe winter with heavy snow from late October to middle April is mainly responsible for the shortening of active period. Among the peculiarities, given above special attention must be paid to the relation between the solitary and superindividual stages. The prolonged solitary stage causes the production of a large number of cells by the founding queen. The tendency to the production of more cells in the solitary stage was also reported under adverse conditions (Morimoto, 1954 b) in *chinensis*. In and near Sapporo, each founding queen constructs more than the half of total cells produced by the colony and rears a not negligible portion of reproductives. In other words, everything necessary for the production of the next generation is qualitatively achieved in the solitary stage, resulting in the reduced significance of superindividual stage, which



approximately corresponds to the expansion phase by Spradbery (1965). The fact results in the reduced production of workers which is comparable to the observations in bumblebees in high altitude (Reinig, 1932) and high Arctic (Sparre-Schneider, 1909, and Richards, 1927). Yoshikawa (1962 c) assumed that workers would not or hardly be produced in polistine colonies at the northern limit of their distribution, leading to the practical omission of the superindividual stage. In the present study, the superindividual stage was confirmed by the production of workers, however, scarce in number. It is still unknown whether the worker production completely ceases in the populations at the real northern limit of the

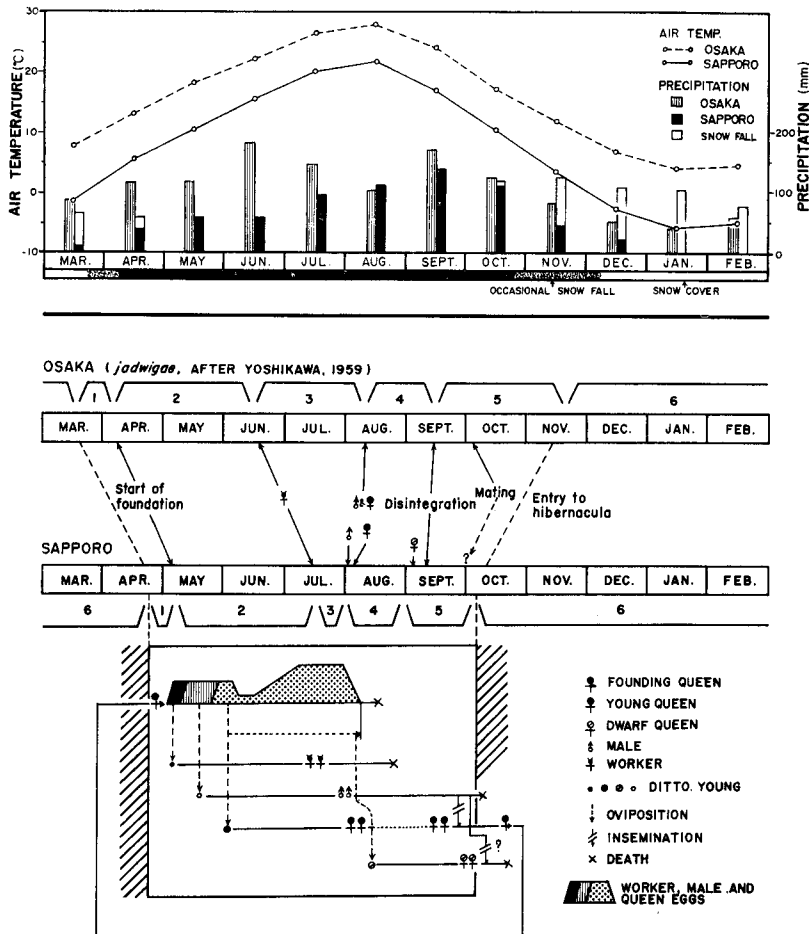


Fig. 9. Comparison of two types of life cycle of *Polistes* wasps between southern and northern Japan with climatic data. 1. Post-hibernant stage, 2. Solitary stage, 3. Superindividual stage, 4. Social stage, 5. Pre-hibernant stage, 6. Hibernant stage.

distribution. However, the reduced significance of this stage in and near Sapporo is obvious from the observations given in the present paper. The most important feature which characterizes the superindividual stage in so-called social insects is the functional division of labor among reproductives and non-reproductives, the former specializing to egg laying, while the latter performing all other tasks. In the present study, no detailed functional analysis was undertaken. But the performance of foraging, cell construction, etc. by the founding queens continued throughout the stage, even though less intensively than in the solitary stage. Further the contribution by workers for the maintenance and development of colonies was very small. Consequently, it is concluded that superindividual stage exists in and near Sapporo only *formally*, but *practically* obsolete, by short duration, absence of sharp functional division of labor, and poor contribution to colony expansion.

The prolonged hibernant stage is compensated by the shortening of three other stages, post-hibernant, superindividual, and pre-hibernant stages, which are seemingly less essential than other stages for the maintenance of the species. For instance, if the founding queen is engaged only in worker production in the solitary stage as in southern Japan, the short favorable season makes the production of reproductives, consequently, the perpetuation of the species, difficult. The only way to maintain the species is to keep the production of necessary amount of reproductives, in the sacrifice of superindividual stage, which is, however complicated and unique among insects, a mere byproduct in the evolution of insect life system. Although these polistine species found the way to survive under severe climate by the passive adaptation mentioned above. It is certain that they do not form a successful group here. This is clearly shown by their numerical inferiority, especially in comparison with *Dolichovespula* and *Vespula*, predominant in the central to northern part of north temperate regions, positively adapted to severe climate by the development of the nest architecture and other possible ways. Simple statistics show this fact. Only three out of seven *Polistes* species in Japan are distributed in Hokkaido, while all six Japanese species belonging to *Dolichovespula* and *Vespula* are common in this district. The similar fact is recognized in both Europe and North America. In Europe three out of seven *Polistes* species are distributed in central Europe, but only one of them reaches Scandinavia, while all seven *Dolichovespula-Vespula* species are common in northern Europe including Scandinavia (Zimmerman, 1930, and Blüthgen, 1961). In North America only one out of 13 *Polistes* species (or two out of 30 subspecies) reaches southern Canada, but eight out of nine *Dolichovespula-Vespula* species (or 11 out of 16, if various previous subspecies are regarded distinct species as in Miller, 1961) are known from Canada and Alaska (Richard, 1951, and Krombein, 1958, '67).

Further functional analyses of various groups of social wasps under different climate may greatly contribute to have a more unbiased perspective of the mode of life of this peculiar group, the studies of which have so far been confined to a

limited number of middle temperate species.

### Summary

1) The outline of the life history of two polistine species (*Polistes snelleni* Saussure and *Polistes biglumis* (Linné)) was studied under natural condition in the vicinity of Sapporo situated near the northernmost margin of north temperate region.

2) No essential difference in the life cycle was observed between two species, but some presumable specific differences were noticed concerning some ethological characters.

3) The comparison of the life cycle with that of polistine species studied in southern Japan revealed the presence of six stages proposed by Yoshikawa in northern Japan, too.

4) However, the relative importance of these stages shows a conspicuous difference. In northern Japan, the hibernant stage is greatly lengthened, apparently caused by severe climate. As a compensation for it, three stages, pre- and post-hibernant stages and superindividual stage are considerably shortened.

5) The reduction of superindividual stage, that is, the period since the emergence of the first worker to that of the first male, is of particular interest. This stage continues only a week, and the number of workers produced is very small. Moreover, some males and young queens are reared by the founding queen, even within the solitary stage, and presumably no sharp division of labor occurs between the founding queen and workers. Consequently, the superindividual stage exists only *formally*, obsoleted *practically*.

6) In both species, the ratio of workers, males, and young queens produced in successful colonies is about 2:3:8, markedly different from that in southern Japan (8:1:1). In both species, the queens produced later are smaller, often even than workers, caused by adverse thermal and nutritional conditions. Such dwarf queens seemingly do not function as the founding queens in the next year.

7) Both species live in hilly and submontane areas and make their nests at relatively open and well insulated places. A tendency to nest site segregation was observed when both species nested in the same area, although further observations are required.

8) In both species, the cell construction in the solitary stage decreases after the hatching of larvae either completely (*biglumis*) or partly (*snelleni*). In *snelleni*, the rate of construction conspicuously recovers after the cocoon spinning by old larvae. Start of the cell construction partly correlates to the absence of empty cells in *snelleni*, but not so strictly as asserted by Deleurance in *P. gallicus*. In *biglumis*, such correlation is practically absent, which suggests the specific variation of this character within the genus.

9) Oviposition rate in solitary stage also decreases after hatching of new larvae and again increases after cocoon spinning by old larvae. The specific difference in this tendency is not so conspicuous as in cell construction. Therefore,

a synchronism between two performance exists in *snelleni*, not in *biglumis*.

10) Some minor specific differences were observed: Deposition of nectar drops into cells (*biglumis*, practically not in *snelleni*); Reuse of cells once produced adults (*biglumis*, not in *snelleni*); Male production (all emerged in late July in *snelleni*, some of them toward the end of colony in *biglumis*); Total adults per total cells produced (higher in *snelleni*, than in *biglumis*); Aggressive behavior shown by young queens (*snelleni*, not in *biglumis*).

11) Some notes on unsuccessful nests of *snelleni* showed that more than 80% of total nests founded were abandoned in the solitary stage mainly by the evacuation, suggesting that this stage is a critical period in the annual cycle.

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