Life Cycle and Nest Architecture of *Polistes* Wasps in the Okushiri Island, Northern Japan (Hymenoptera, Vespidae)[1][2]

By

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(*With 9 Text-figures and 2 Tables*)

The Okushiri Island, lying in the Japan Sea about 18 km west from Setana, southern Hokkaido, has four *Polistes* species (Munakata and Yamane, 1970), but their biology and sociology have so far not been studied. Of four species, *P. chinensis antennalis* Pérez is the commonest, *P. rothneyi iwatai* Vecht is the next, and the other two, *P. mandarinus* Saussure and *P. snelleni* Saussure are rare. It is important to study the life mode of two common species at their northern limit of geographical distribution, in reference to social structure and adaptation at the cool temperate region. In my previous paper on the outline of the life history of *P. snelleni* and *P. biglumis* in Sapporo, the latter of which may be the northern vicariant of *P. chinensis,* it was supposed that the number of worker is smaller and the period of the superindividual stage defined by Yoshikawa (1962a) is shorter than in populations in southern Japan, presumably because of reduction of the duration of nesting activity due to the cooler weatheer (Yamane, 1969a). In the present paper the life cycle and nest architecture of two species mentioned above are described and briefly discussed in comparison with those obtained from populations in southern Japan and two different species in Sapporo, based upon two surveys in June and September, 1970, and rearing of *chinensis* colonies in Sapporo.

Before going further, I wish to express my sincere thanks to Dr. Shôichi F. Sakagami of the Zoological Institute, Hokkaido University, for his kind guidance in the course of the present study. Cordial thanks are also due to Assist. Prof. Meiyô Munakata, Hokkaido University of Education and Mr. Sadaharu Ikejima, Okushiri Town, for their helps at my stay in the Okushiri, and to Prof. Mayumi Yamada, Zoological Institute, Hokkaido University, who kindly read through the manuscript.

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1) Contribution No. 930 from the Zoological Institute, Faculty of Science, Hokkaido University.

2) Biology and sociology of *Polistes* wasps in Northern Japan. III.

Areas surveyed

A schematic map of the Okushiri Island and surveyed routes are given in Fig. 1 (cf. also Munakata and Yamane, 1970). The surveys were made as follows. The first survey (June 20 ~22) at Okushiri Town, Bushigawa, a pass between Miyatsu and Nonamae, Inaho, and Akaishi. The second survey (September 7–10) at a pass between Okushiri T. and Horonai, Coast of Horonai, Aonae, Inaho Point, Inaho, Nonamae, Akaishi, and Bushigawa.

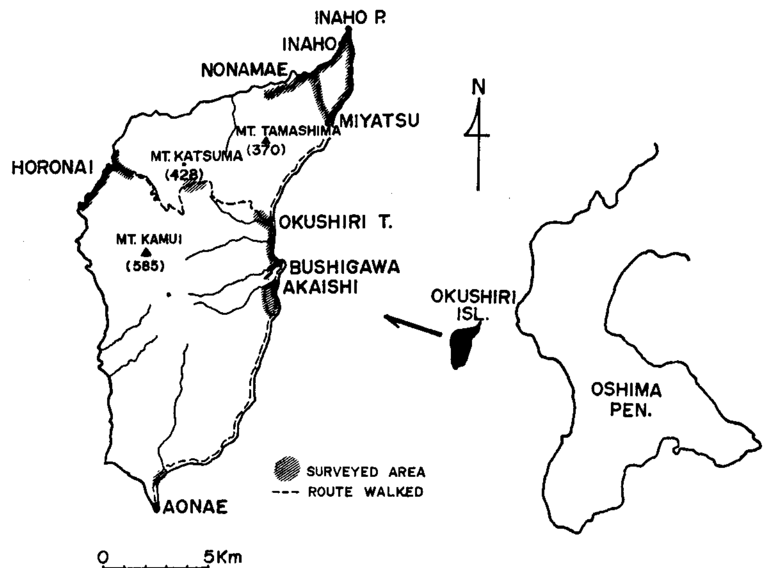

Fig. 1. A schematic map of the Okushiri Island showing routes of surveys.

1. Distribution and nesting sites

Both species seem to inhabit mainly narrow coastal plains and their terraces, but rarer in central submontane areas.

The nesting sites were recorded as follows: *A*) *P. chinensis*: Nests were found mostly at open places: Bushigawa: trunks of afforested young Japanese cedar (1 ~3 m high), stems of mugwort *Artemisia* sp.; Akaishi: young Japanese cedar, twigs of gooseberry, trunks and twigs of shrubs; Inaho-Nonamae: young Japanese cedar, twigs of sweet brier *Rosa rugosa*, stems of mugwort; Horonai: sweet brier. The plants on which the nests were attached are shown as the following descending order: young Japanese cedar (13 cases, 10 on trunks and 3 on twigs) sweet brier (7), withered stems of mugwort (6), withered stems of dock *Rumex* sp. (2), stem of daisyfleabane *Erigeron annus* (1), reed *Fragmitis* sp. (1), twig of oleastern *Elaegnus* sp. (1), twig of *Malus* sp. (1), Sachaline giant knotweed *Polygonum sachalinense*

(1), twig of weigela *Weigela hortensis* (1), withered stem of bamboo *Sasa* sp. (1). Besides plant substrates, one nest was found on the under-side of a rock. Thus, nesting sites are similar to those of *P. biglumis* in Sapporo and Oketo. Although nests of this species are generally found under eaves of the house, at crevices of tiles covering the roof, on walls, etc. in southern Japan, no such cases were seen in the present survey. Nests usually attach to the plants of 30 ~100 cm high, rarely to those more than two meters, and attach at the level less than 100 cm above the ground (Fig. 2), with the axes horizontally or aslant to downward as in *P. biglumis* (Fig. 4A, B, D, E), and *P. chinensis* nesting on perpendicular substrates in southern Japan. *B*) *P. rothneyi*: Eight nests were discovered at a small village consisting of thirteen houses only about 30 m distant from the coast line of Horonai. Nests were hung down on eaves of the houses as commonly seen in southern Japan. This species seems to make the nest usually on such a place at everywhere in the island.

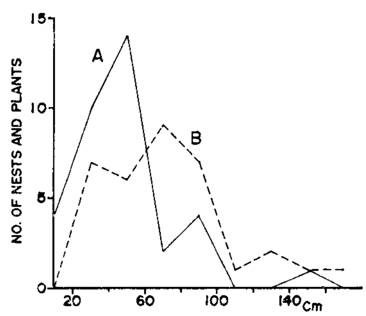

Fig. 2. Heights of nest (A) and plants used as nest substrates (B).

2. Records of nests observed

Twenty-eight nests, three of them having been orphan, and twelve ones of *P. chinensis* were discovered in June and September respectively. Ten out of them found in June were carried to the garden of the Apicultural Laboratory of Hokkaido University, and those found in September as well as five out of seven nests of *P. rothneyi* were sampled to examine their nest composition.

2.1 *P. chinensis*

2.1.1. Observations on June 20 ~22: *A*) *Developmental stage of nests* (*Tab. 1*): Except for three orphan nests, developmental stages of 25 nests were all in the solitary stage, from just after the foundation (OI 7001) to cocoon stage (OI 7027), though mostly of just before and after the appearance of larvae. The foundation is crudely estimated late May to early June for most nests, middle May for the earliest one (OI 7027), judging from the duration of egg and larval stages taking 35 ~45 days in other species in Sapporo. Dates of nest foundation in this island are about 1.5 months later than in southern Japan (Osaka and Wakayama, middle April; Fukuoka, early April).

B) *Number of cells made in solitary stage*: The construction of new cell decreases or nearly ceases after the appearance of larvae (Morimoto, 1954b, Yamane, 1969a). Therefore, the total number of cells constructed by a founding queen in

Table 1. Nest composition of *P. chinensis* in the Okushiri Island on June 20～22, 1970.

Nest No.	Total cells (Tc)	Eggs	Larvae						Cocoon	Vacant cells (Vc)	Vc/Tc	Remarks
			1st	2nd	3rd	4th	5th	T				
OI 7001	4	2								2	0.500	
02	23	19								4	0.174	
03	38	25	2					2		11	0.290	
04	36	23								13	0.361	
05	28	18								10	0.357	
06	36	26								10	0.278	
07	4											Orphan
08	36	17	2	2				4		15	0.417	
09	34	14	3	1				4		16	0.471	
10	43	24	2					2		17	0.396	
11	38	18								20	0.526	
12	43	15	4	1	2	1		8		20	0.465	
13	42	9	1	5	2			8		25	0.595	
14	32	18								14	0.437	
15	43	19	4					4		20	0.465	
16	48	9	3	2	2	5		12		27	0.562	
17	43	10	6	1	2	2		11		22	0.511	
18	21	15								6	0.286	
19	35	24								11	0.314	
20	28	21	2					2		5	0.177	
21	39	27	1					1		11	0.282	
22	ca. 30											Orphan
23	42	23	2	1				3		16	0.381	
24	46	13	4	4				8		25	0.545	
25	45	24	5					5		12	0.293	
26	31											Orphan
27	39	9	3	3	1	2	5	14	1	15	0.385	
28	35	11	5	1	2			8		16	0.457	

the solitary stage might mostly be represented by those constructed before the appearance of larvae or by those with some minor additions.[1] Therefore, the total number of cells constructed in the solitary stage is estimated at 30～50 in the island, slightly higher than in Fukuoka (30～40, Morimoto 1954a) and Wakayama (20～40), but less than in *P. biglumis* in Sapporo and Oketo (50～70).

C) *Vacant cells at periphery of nest*: In early period of solitary stage, only cells locating at central part are used for rearing immatures. Peripheral cells are left vacant or, if used, only for storing nectar drops (Fig. 3A). The vacant cells ranged 4～25 (mean 15 with 23 nests), or the ratios to total cells (Vc/Tc), 0.177～0.595 (cf. Tab. 1, mean 0.393), showing that nearly a half of total cells were left

1) After the appearance of larvae, cell increase nearly stops in most nests of *P. biglumis*, while not completely, continuing slowly in *P. chinensis* (Fig. 5A).

vacant at least in nests observed.[1)]

2.1.2. Observations on September 9 and 10: *A*) *Number of total cells constructed* ranged 23∼99 (mean 58.6 for 11 nests, excluding a reconstructed one OI 7036). More smaller nests were discovered at a shrub and sweet brier area in Inaho Point than at afforested areas, etc. locating distant from coastal lines, seemingly affected by exposure to the direct sea breeze. Number of total cells counted at sampling (Tab. 2, shown as total cell number) may approximately be regarded as those constructed throughout the year, since the cell increase after the sampling dates is hardly conceivable, even if the nests were left in intact. Even the maximum number obtained for OI 7044 made on Japanese cedar does not exceed 100, showing the limit of nest development in this island compared with southern populations making larger nests with 200∼500 cells, or rarely more than 800 (Morioka, Wakayama, etc.). At the same time, the comparison of Table 1 and 2 shows that the number of cells constructed by the founding queen occupies a considerable part of the total number produced throughout the seasons.

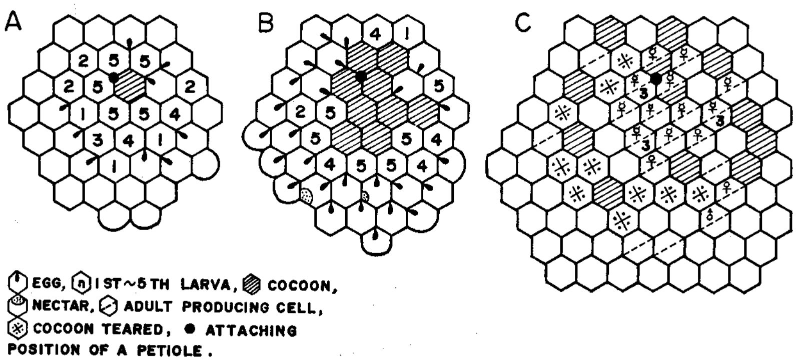

Fig. 3. Cell map of OI 7027 reared in Sapporo at various stages. A. in solitary stage, B. just before the first worker emergence, and C. near disintegration of nest.

B) *Life stage*: Adults had already emerged in all nests. Only one out of eleven nests had the founding queen and seven with a worker or workers, showing that the superindividual organization had broken up in most nests at the time of observation. Seven out of eleven nests had produced males and new queens, and a portion of them had already dispersed from the nest, judging from the small

1) The real number and Vc/Tc change according to the progress of nest development, reaching the maximum nearly at the time of the first appearance of the larva. Only nests whose developmental stages did not extremely deviate from the condition at which the maximum could be attained, were used for examination. Two nests (OI 7001 and 7027) were excluded for not satisfying above.

number of adults presented, and, on the contrary, the presence of a lot of cocoon traces. Only one nest OI 7038 had still eggs, five nests larvae, seven ones cocoons, and four were completely empty, though some adults still attached to them. Those facts suggest the colony disintegration had commenced in most nests.

C) *Frequency of use of one and the same cell*: It is interesting to know how many times one and the same cell is used for rearing immatures and produces adults. This requires regular and continuous observations, but cocoons found at the central part of nests in OI 7038 ~7040 and 7042 seem to be the second batch by the following reasoning: if the nests were founded in early June, and the total duration of immature stages takes 50 ~60 days for the first worker (cf. Yamane, 1969a), it may emerged in late July to early August. If the cells were occupied immediately with eggs, the presence of cocoons by the dates of observation in early September (eggs to cocoon stage, about 25 days) is not always impossible. Examination of the faecal pellet left at the bottom of cell also suggests the presence of the second use of one cell. Although further evidence is required, the result from a nest (OI 7027) transplanted to the University Campus suggests the second use of one and the same cell for brood rearing is not rare in this species, even if these cells may not always produce adults.

D) *Total adults produced*: Table 2 gives numbers of cells ascertained to have produced adults, judging from the presence of cocoon traces. These traces must approximately be equal to total adults produced, as the number of adults of the second batch must be few, and even if produced, the destruction of cocoons by adult inhabitants and parasitism on pupae by other insects must reduced the real number of total adults. The number of workers is small, perhaps within fifteen even in large nests, judging from the result of OI 7027. But, that of each male or new queen is quite variable with nests. At any rate, the maximum number of total adults seems far less than a hundred in nests collected. Total numbers obtained are considerably smaller than those in southern Japan where colonies often produce more than one hundred workers and hundreds in total adults.

E) *Nest reconstruction*: Polistine wasps often reconstruct nests after the evacuation or when the nests are destroyed by wind, rain or natural enemies: *P. biglumis* (Oketo, Kawamichi and Yamane, unpublished), *P. jadwigae*, *P. rothneyi* and *P. chinensis* (Wakayama Pref., Matsuura, Yamane, etc., unpublished). But the case on *P. chinensis* is still unknown in Hokkaido and its adjacent islands. The Nest OI 7036 had three workers inspite of the absence of any cocoon traces, showing the reconstruction after worker emergence. Based upon the developmental stage of immatures, the nest seemed to have been reconstructed in middle or late August. It has normal architecture with a petiole and a comb, like as those made at usual nest foundation in spring.

2.2. P. rothneyi (*September 7 ~9, Tab. 2*): *A*) *Number of cells*: One out of five nests sampled was already orphan. This nest OI 7045 had eleven cocoon traces, seemingly been abandoned or destroyed just before or after the worker

Table 2. Nest composition of *P. chinensis* and *P. rothneyi* on September 7～10, 1970.

Nest No.	Total cells	Eggs	Larvae						Cocoons					Closed cells	Adults on nest					No. of adults producing cells
			1st	2nd	3rd	4th	5th	T	☿	♀	♂	?	T		**♀**	☿	♀	♂	T	
P. chinensis																				
OI 7029	66										1	1	2				3	4	7	20
30	70		1				1	2		2	12	2	16			1	5	1	7	23
35	63													2			12	1	13	31
36	38	19	4					4								3			3	Reconstructed
37	31		1				4	5				3	3	3		1			1	>3
38	52	3					9	9		4	7	4	15		1	1	1	2	5	>8
39	23		1			1	2	4				5	5	3		1			1	1
40	60			1			2	3		3	8	2	13			5			5	7
41	57			1				1									5	2	7	16
42	48			1			3	4		6	2	6	14			4			4	>2
43	75																17		17	45
44	99																7	7	14	58
P. rothneyi																				
OI 7031	135			1	1		6	8		1	28	13	42			3	7	18	28	70
32	52										8		8					10	10	37
33	137	2		10	5	4	11	30		2	23	12	37				9	34	43	66
34	16	2	1	4		11	2	8										6	6	11
45	29																			Orphan

♀. Founding queen, ♀. New queen.

emergence. Number of cells made in the solitary stage seems to be 29 or slightly less. In other nests, numbers of cells range 16 ~ 137 at the time of sampling. Nest OI 7033 with 137 cells may represent nearly the maximum attained in this island. Of four nests, OI 7034 with 16 cells seems to be of particular case for the sake of the absence of workers, not for dispersal, for not to have been produced.

B) *Life stage*: In all nests except for OI 7045, males had emerged and in two largest nests (OI 7031 and 7033) new queens had also emerged. All nests had lost their founding queens and only one (OI 7031) had workers. Larvae and eggs were absent or scarce, but the presence of many cocoons suggested the continuation of nesting activity, if they were left in intact. The life stage of these nests corresponding to the social to prehibernant stage of Yoshikawa's classification.

C) *Nests with adult males alone*: Some interpretations are given to Nests OI 7032 and 7034 with only males as adults. *OI 7032*: 1) Workers and new queens emerged, but dispersed in early period. 2) The founding queen could not lay fertilized eggs. If the case was so, 52 cells presented were all due to the founding queen which remained for a while at the nest after the emergence of males. 3) Escape of the queen and workers from sampling by their outdoor activities is less plausible because no returning individuals were captured after nest sampling. The second case is the most probable, although the other two can not be entirely negligible. *OI 7034*: The coincidence of numbers of cocoon traces and adult males, both six, presented properly shows the absence of workers in this nest as mentioned in *2.2.A*.

D) *Frequency of cell re-use and total adults produced*: The second use of one and the same cell was observed in Nests OI 7031, 7033 and 7034, although the method of re-use in this species is quite different from that in *P. chinensis*. After the egg was deposited on the pre-existing cocoon, the pupa within the latter transforms to the adult when the former attains to the third or fourth instar, and takes the way through the side of the younger sib by pressing it to the cell wall. Such a method is also adopted by *P. jadwigae*, a southern Japan species belonging to the same subgenus *Megapolistes*. It is, however, still unknown how many cells were used for the second brood rearing, inspite of possible larger number than in *P. chinensis*, because of the advantage of preceding use before eclosion of adult. Total adults produced seem to exceed one hundred in the largest nests. It is certain that males produced were most abundant, though the accurate sex and caste ratios were not determined.

3. Nest architecture

3.1. P. chinensis: As described in *2.1.2.*, nests in Okushiri are smaller than in southern Japan. Besides the size, some conspicuous differences exist as to nest architecture as enumerated below in comparison with those from southern populations and *P. biglumis* in Sapporo and Oketo. 1) Petiole attaches to nearly the

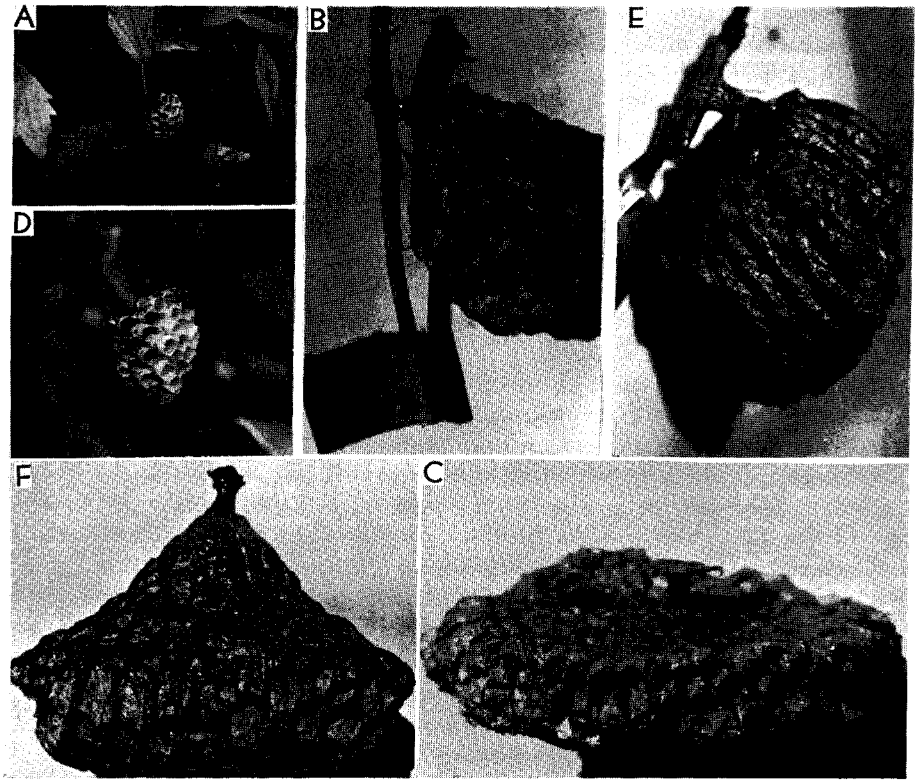

Fig. 4. A and B. Early and later nests of *P. chinensis* in Okushiri, and C. later nest of the same species in Wakayama, D and E. later nests of *P. biglumis* in Oketo, F. later nest of *P. rothneyi.*

uppermost part of the comb as in *P. biglumis*, while nearly at the center of the upper surface in southern Japan (Fig. 4B, C, E). 2) Frontal shape of the comb varies from oval to oblong, the latter being more frequent as in *P. biglumis*, while mainly circular in open places in southern Japan (Fig. 5A a-c). 3) Irregularly shaped and incomplete cells are constructed at the lateral sides of the comb as in *P. biglumis*, while such are not seen in southern Japan (Fig. 4B, C, E). 4) Cells are very long except for peripheral ones, ranging 25 ~35 mm at the center at the end of nesting activity, distinctly longer than the cocoon length (15 ~17 mm). The formation of "elongate cell" can be seen already at the appearance of the first cocoon in the solitary stage, being 3 ~5 mm longer than the cocoon length, and the elongation continues even after the formation of the cocoon. The cell length attained at the end of nesting activity reaches 17 ~25 mm in southern Japan, and

30 ~45 mm in *P. biglumis* (Fig. 4B, C, E, 5B a ~f). 5) As mentioned above, the architecture of nests from Okushiri rather resembles in most aspects that of *P. biglumis* than that of the conspecific populations in southern Japan. The features of nests of *P. chinensis* in Okushiri differ from those of *P. biglumis* in the relatively smaller size and convex contour of comb surface in cross section due to gradual decrease of cell length from center to periphery.

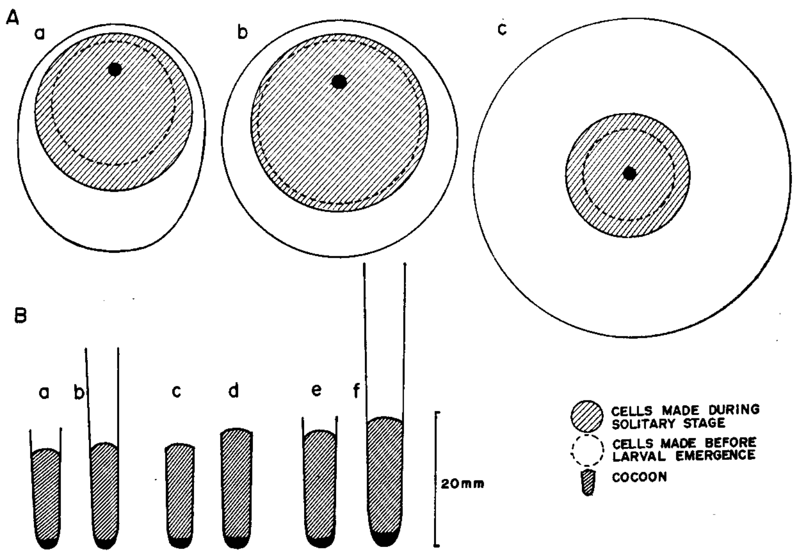

Fig. 5. A. Frontal shape of nests with growing lines. a and c. *P. chinensis* in Okushiri and at open place in Wakayama, b. *P. biglumis*; B. Relation between lengths of cell and cocoon. a and b. early and later cells of *P. ch.* in Okushiri, c and d. early and later, ditto in Wakayama, e and f. early and later in *P. b.*

3.2. *P. rothneyi*: As in southern Japan, nests are of hanging bell shape (Fig. 4F). After cocoon formation cells are elongated 5 ~10 mm beyond the top of the cocoon. Such over-elongation is also common in southern populations, as well as in a related species *P. jadwigae* in southern Japan, and its significance may be different from the similar tendency in *P. chinensis* as discussed later.

4. Observations on transplanted *chinensis* colonies in Sapporo

Nests removed from their former nesting sites (OI 7010 ~7017 on June 21 '70 and OI 7027, 7028 on June 22) were carried back to the garden of the Apicultural Laboratory, Hokkaido University, Sapporo in the evening of June 23. During the trasport queens were separated from their nests to prevent eating immatures. On June 24, six nests, OI 7010 ~7013, 7016, 7017, and 7027, were attached to twigs with the nest axes kept horizontally by adhesive and twine. Each of them was accomodated in a box ($22\times26.5\times51$ cm^3) with two wire-netted sides made for the transport of honey bee hive. The box was left overnight with a lid closed. The queen of OI 7028 was substituted for OI 7027, because of the death of the legitimate queen in the latter. After the removal of lids of boxes in the morning of June 25, queens of OI 7010, 7012 and 7013 flew away and never returned again. In only three nests the queens remained for a while, and in only one OI 7027 till the worker emergence. Therefore, all results mentioned below were taken with Nest OI 7027. It was, as a rule, observed once per day near or after the sunset to map the daily change of nest development, besides occasional observations on activities of the colony.

4.1. Emergence of adults: *A*) *Workers*: The first worker emerged on July 13 from the cocoon made on June 23, the cocoon stage then lasting 21 days. Additional ten workers emerged by August 1 (Fig. 6). The duration of their stay on the nest varied from four (☿2) to more than 52 days (☿1), except for two cases induced by artifact: where ☿3 escaped walking out from the nest immediately

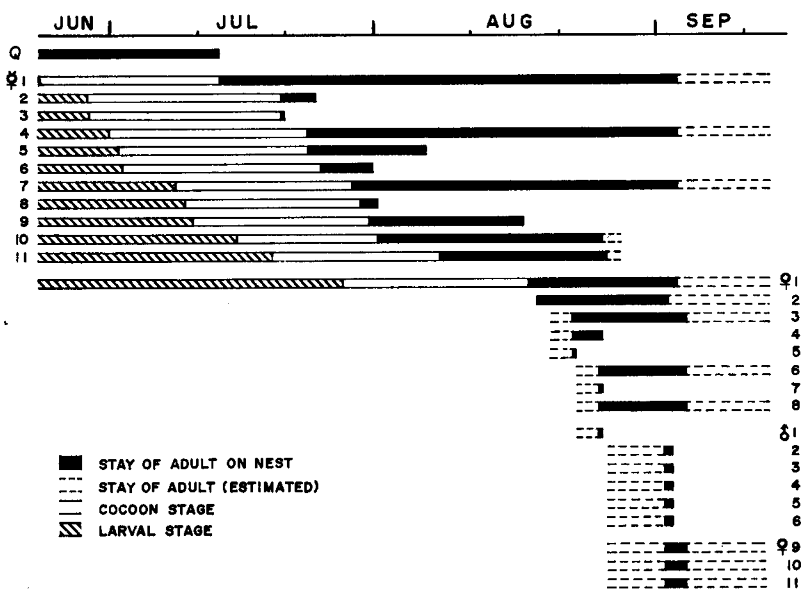

Fig. 6. Dates of adult emergence and duration of their stay in Nest OI 7027, with period of cocoon stage.

after marking[1] and ☿8 was driven by its mates probably for the damage of fore wing evoked at marking. ☿2 failed to return after the orientation flight. The minimum duration from the emergence to the dispersal was six days among workers which had succeeded in the orientation flight. *B*) *Males*: Six individuals emerged during August 29 and September 1, staying at the nest for several days and, then spread away, but with occasional flights around the nest in early September. *C*) *New queens*: Eight individuals emerged on August 16～25 and five on August 29～September 1, thirteen or slightly more in total. Most of them stayed till the entire disintegration on September 13.

OI 7027, reared for observations was the most advanced nest among those discovered in late June. Other nests contained at most the fourth instar larvae, suggesting the emergence of adult workers at late July in them. Total adults produced in OI 7027 reached little more than 30 (11☿ and 9♀♂, 20 in total by the legitimate queen and more than 10♀♂ by the substituting queen). Worker-born eggs did not grow to adults because of frequent oo- and larvophagy by workers, seemingly caused by an unstable orphan situation.

4.2. Cell multiplication: *A*) *By the founding queen*: The cell multiplication after the transplantation began on July 3, rather sporadically one cell or more (maximum, 5 per day) on alternate days (Fig. 7D). Fourteen cells were added by the queen during her stay at the nest till July 13. The new cells were made chiefly on days when apparent vacant cells were absent or a few (July 10, 11 and 13), although a small portion (5 out of 14) was made on other days, too. This phenomenon suggests the presence of a loose synchronization between oviposition and cell multiplication, allowing an application of "La régle des cellules libres"[2] proposed by Deleurance (1957) at least in the period at or near the first worker eclosion (Fig. 7D, E). *B*) *By workers*: On the seventh day after the first worker emergence, one new cell was made by a worker, but full scale activity was noted during July 27 and August 2. Thirteen cells were made irrespective of the presence or absence of apparent vacant cells. At least six workers, ☿1, 4, 5, 7, 9 and 10, participated in constructing activities involving the petiole reinforcement, cell multiplication, and cell wall elongation.

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1) Newly emerged individuals before the performance of orientation flight, sometimes walk around the nest erratically and at last escape or fall down from the nest after removing from it and subsequent reattachment to it. This tendency is more frequent in *P. snelleni*, *P. jadwigae*, etc., the species making the hanging type nest with a vertical nest axis. If such the case would happen, the detected individual must be reattached gently. In hanging type nest, it is effective to prevent such "escape out" by setting the nest temporarily upside-down or nearly so.

2) A rule noting that a female restarts the construction of new cells when vacant cell becomes absent. The presence of this rule was confirmed in the solitary stage of *P. snelleni* (Yamane, 1971) and *P. jadwigae* (Yamane, unpubl.), but not in the early solitary stage of *P. biglumis* (Yamane, 1969a, 1971).

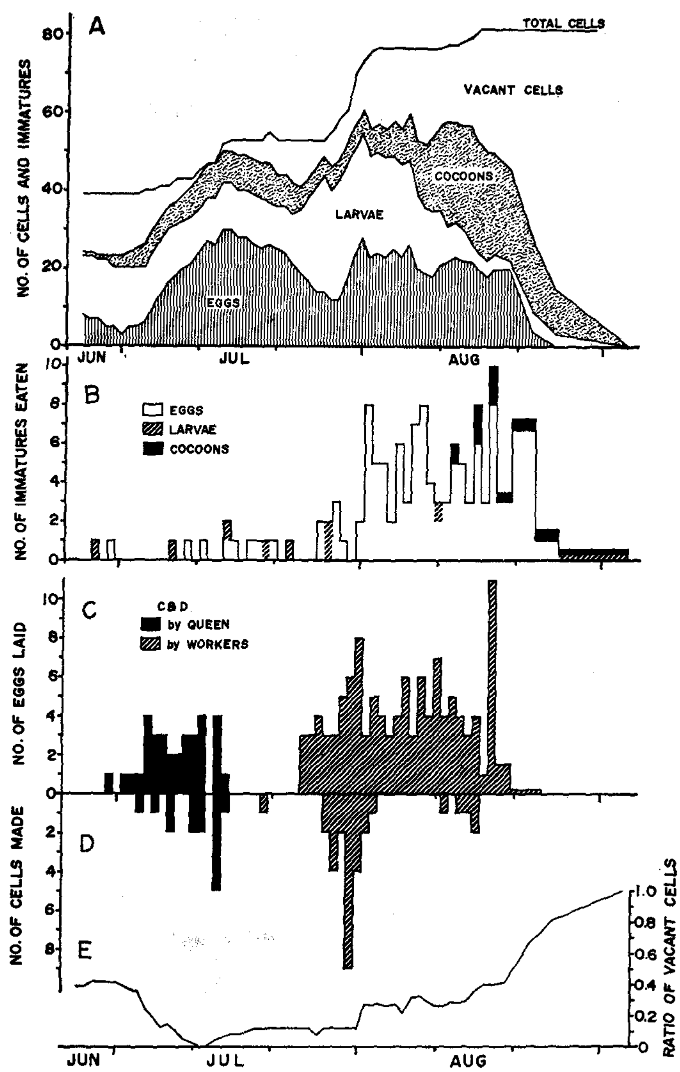

Fig. 7. Observations on Nest OI 7027 transplanted from Okushiri to Sapporo. A. Immature populations, B. Frequency of cannibalism, C. Freq. of oviposition, D. Number of cells constructed, and E. Changes in the ratio of vacant cells (Vc/Tc).

4.3. Oviposition: *A*) *By the founding queen* (*Fig. 7C*): She started oviposition activity on June 29 and continued it until her disappearance on July 12, laying 1 ~4 eggs per day except for June 30 and July 12. At the start of oviposition activity, 27 immatures produced by the legitimate queen were present.

B) *By workers* (*Fig. 7C*): This nest was maintained without any critical and serious damages to immatures after disappearance of its queen for the sake of the worker activities. Oviposition activity after queen disappearance is, therefore, all due to workers. The first oviposition was done on the twelfth day from the first worker emergence perhaps by her. Henceforth, eggs were laid every day (max. 11 eggs/day, mean 3.6/day, and 118 in total) by single or pleural individuals. Ovipositions by pleural workers on the same days were not confirmed, but were highly probable. On August 6 ☿1 was about to lay an egg inserting her abdomen, although the activity was interrupted by certain stimulations. Nearly synchronously, ☿7 was just in oviposition a little remote from ☿1. Therefore, the contemporaneous ovary development among pleural workers is certain. The presence of simultaneous oviposition even in normal nest with a queen and workers in this species and in *P. biglumis* also confirms the ovary development in more than one inhabitant. This fact might show the lack of any marked inhibition of ovary development and oviposition behavior among individuals seen in other polistine species. Many "super-numerary eggs" (cf. Duncan, 1939) were observed at each cell after the worker emergence.

4.4. Cannibalism: This phenomenon is to some degree seen in any healthy nests irrespective of its developmental stage. In this nest, this activity was seen approximately every two days, but after the worker emergence seen every day (Fig. 7B). The maximum number reached ten per day on August 17. The respective total number eaten before or after worker emergence was seven (4 eggs and 3 larvae for 20 days) or more than 112 ($>$101 eggs, 5 larvae and 6 cocoons for 36 days). Apparently this high frequency cannot be explained simply by the increase of workers. No worker-born eggs produced adults because of frequent cannibalism, showing the abnormal condition after the worker emergence. The absence of the founding queen as a stabilizer, may be regarded as a cause, seemingly resulting in increased fights among workers. But, once I observed the normal brood rearing by workers and subsequent emergence of many males from unfertilized worker-born eggs in a transplanted queen-less nest of the same species (Yamane 1969b), suggesting that the cannibalism in orphan nest is not inevitable. As described above, the egg eating activity immediately after the oviposition results in the prolonged occurrence of one but not the same egg in a cell, because of the repetition of eating and oviposition, called "egg persistence" by Brian and Brian (1952). They observed this phenomenon in early nest of *Vespula sylvestris* Scopoli, where the appearance of the larva was markedly delayed for the replacement of eggs causing the serious disturbance of the nest development in the early stage. Cannibalism might occur by several reasons varying with the developmental stage and the particular condition of the nest, and its ecological and sociological significances must differ according to the situation, although the clarification of them is still open for further studies.

4.5. Brood population trend: *A*) *Eggs*: Active oviposition by the founding queen resulted in a peak on July 12 (Fig. 7A), followed by a subsequent decrease by the flow-out of them into larval stage. The second egg accumulation occurred during late July and middle August by worker oviposition, forming a more or less fluctuated plateau with the peak slightly lower than the first one, probably in part because of incessant oophagy. Eggs disappeared on August 24. *B*) *Larvae*: A peak (31 inds.) was attained on July 28 about two weeks later than the first egg peak by its sliding to larval stage. The other peak expected theoretically from the worker oviposition, failed to be attained for the reason as mentioned in the previous section (*4.4.*). *C*) *Cocoons*: A peak (30 inds.) lies on August 14 formed by the individuals flowed-out from larval stage.

4.6. Trend of vacant cells: In late June, at the date of transplantation, the nest had many vacant cells, 40% to total cells at its periphery, as described in *2.1.1.* They gradually decreased with the accumulation of eggs and disappeared at the observations on July 11 and 12, just before the worker emergence (Fig. 3B). Then, vacant cells reappeared (Fig. 3C) and increased to make it completely vacant on September 3, because of successive emergence of adults, the multiplication of cells by workers, later by the cannibalism and decreased oviposition (Fig. 7E). The trend of vacant cells shown in the present nest is not always regarded as a representative pattern, because of the artifacts such as nest transplantation, queen substitution, etc., but the information from other observations well corresponds to my present case that the peripheral vacant cells present in early solitary stage decrease or disappear, that is, the expansion of brood rearing zone at or near the first worker emergence, and re-increase after it (*P. chinensis* in Fukuoka, Morimoto, 1954a; in Wakayama, Yamane, unpublished; and *P. biglumis* in Sapporo, Yamane, 1969a). My fragmentary observations suggest, however, a slight prolongation of the period during which the most part of nest is filled with broods, after the emergence of the first worker, in southern colonies than in northern ones.

Concluding remarks

In previous papers, polistine life in northern Japan was preliminarily studied and some ecological and sociological problems were pointed out (Yamane, 1969a, '71). Marked characteristics shown in Sapporo were as follows: 1) Small colony size as represented by small number of workers, 2) shortened queen-worker association period. Such characteristics must be considered from the point of variability of life system within a species, for the understanding the mode of existence of the species. Although the present paper consists only of fragmentary observations, several features of life mode in northern *Polistes* especially in *P. chinensis* are mentioned for the further comparison of modes between northern and southern populations. In addition, the peculiar nest architecture of *P. chinensis* in Okushiri is considered in respect to its probable adaptation to rigorous environmental conditions.

1. Life cycle: Here the following is given as to life cycle of *P. chinensis* based upon the fragmentary observations. *1*) *Foundation of nest*: OI 7027, the most developed one among 25 nests observed, was founded in middle May, but others one or two weeks later. The former is 1.5 months later than in the same species in Wakayama, three weeks than in *P. snelleni* and *P. biglumis* in Sapporo. Foundation of nests in *P. rothneyi* might occur by middle or late May, judging from the capture of the founding queens already in early May (cf. Munakata and Yamane, 1970). *2*) *Disintegration* occurred in early to middle September, nearly the same as in southern Japan as well as two different species in Sapporo. The disintegration in *P. rothneyi* might occur in middle or late September. *3*) *Duration of nesting activity* is reduced two or three weeks than in *P. snelleni* and *P. biglumis* in Sapporo caused by delayed nest foundation, and 1.5∼2 months than in Wakayama, southern Japan. *4*) *Workers emerge*, but less abundant than in southern populations (presumed as about ten in Okushiri and 10∼50 in Wakayama[1)]). The *rothneyi* nests also produced workers. *5*) *Rearing of reproductives* is presumed to be commenced already in the solitary stage. New queens emerged earlier than males in Nest OI 7027. But it is still open to further observations, whether such a preceding production of new queens is usual in other nests. *6*) *Presence of the superindividual stage* is fairly suggested by the facts mentioned above.

Here, I avoid detailed discussions upon the life cycle, but would like to refer to that the two *Polistes* species in the Okushiri Island can complete the life cycle representative of temperate regions as Wakayama, Osaka, etc., inspite of the presence of some modifications as shown by less workers, etc. caused by rigorous climatic conditions.

2. Nest architecture: The morphological feature of *chinensis* nest in Okushiri has been mentioned in comparison to those from Honshu and of *P. biglumis* from Sapporo and Oketo (cf. *3.1.*). Here I would refer to "elongate cell" produced by northern populations. The tendency to elongate cells appears already at the first cocoon spinning in the solitary stage. The founding queen continues to elongate cell walls 3∼5 mm higher beyond the top of cocoon. Such behavior is also seen in *P. biglumis*, but rarely in southern populations of *P. chinensis*. Cells, especially those at nest center are successively elongated by the queen and workers, reaching about 27∼35 mm long at the end of nesting season. The cocoon occupies only a bottom half of such a cell. The species making such notably elongate cells in Japan are confined to *P. chinensis* and *P. biglumis*, both belonging to the subgenus *Polistes*. The cell elongation is also known in *P. rothneyi* and *P. jadwigae*,

1) The number given is based on my observations. It may attain sometimes more than a hundred in southern Japan.

belonging to the subgenus *Megapolistes*, but here the elongate cell is useful for the simultaneous rearing of a brood at the cell preoccupied by a cocoon. As far as I am aware, the habit same to *P. chinensis* in Japan is known in *P. chinensis* (=*Polistula chinensis*), *P. biglumis bimaculatus* (=*P. Kholi*), *P. foederatus* (=*Polistula foederata*), and *P. ommisa* (=*Polistula ommisa*) in Europe, Northern Africa, Medeterranean areas, and West Asia (Weyrauch, 1939). These species are all closely allied to *P. chinensis* and the elongate cell seems to be a group characteristic than to their geographical especially latitudinal distribution. But interestingly *chinensis* nests from southern Japan have only short cells well corresponding to cocoon length, contrasting to the formation of elongate cells by northern populations. This fact might show the local variability of nest morphology within the species and might indicate the pressence of ecological merits by elongation of cells in northern districts, although no study exists on the presence of same tendency in occidental populations. *P. biglumis* occupies the northernmost part of polistine distribution in the Palaearctic region (*eg.* Scandinavia, alpine regions in northern Europe, Sachaline, Kurile Islands, and Hokkaido), where the elongate cell might be useful for keeping the cell temperature, although further studies must be carried out to elucidate its origin and function.

3. Vacant cells: The presence of "vacant cells" at peripheral part of the nest in early developmental stage has already been demonstrated. Such a habit is seen also in southern populations of this species, *P. biglumis* (Sapporo and Oketo) and *P. biglumis bimaculatus* (alpine regions in Europe, Steiner, 1929), all belonging to the same subgenus. The occurrence of this characteristic is possibly assumed also in some other species, inspite of absence in *P. gallicus* with which "La régle des cellules libres" was proposed.

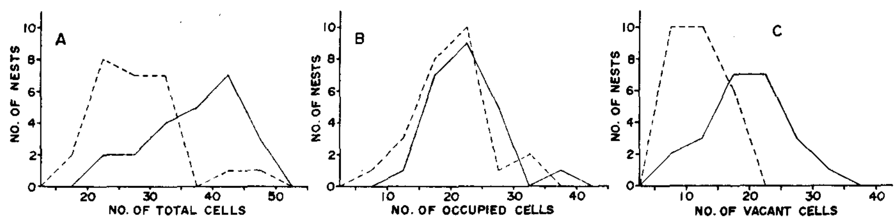

Fig. 8. Comparison of number of cells in *P. chinensis* in Okushiri and Wakayama nearly at the period of larval appearance. A. Number of total cells, B. No. of cells occupied by broods, and C. No. of vacant cells.

Here are referred to some differences of nest utilization in populations between Okushiri and Wakayama, although the information is still premature to discuss the significance of vacant cells. The comparison is made using the nests lying at the developmental stages from the appearance of larvae to that with middle aged ones when the higher values for vacant cells are expected. The comparison of nest from two localities applying t-test (level of significance=1%) revealed the following facts: A) The total cells produced by this stage is significantly abundant in Okushiri than in Wakayama (m=37.36±3.19 with 23 nests in Okushiri and 27.85±2.87 with 26 nests in Wakayama, Fig. 8A). B) The number of cells occupied by brood is nearly equal between two localities (m=22.21±2.08 in Okushiri and 21.19±2.18 in Wakayama, Fig. 8B). C) The number of vacant cells is significantly more abundant in Okushiri (m=15.04±2.75) than in Wakayama (m=6.65±1.94) (Fig. 8C). Fig. 9, dealing with a relation between the numbers of vacant and total cells gives a tendency that the vacant cells are more abundant in large nests in Okushiri, but not always in Wakayama. Another fact noticed is the virtual obsoletion of vacant cells in some Wakayama nests. Simply contrasting to nests, practical obsoletion is not recognized in Okushiri. Since the number of broods reared at nearly the appearance of larvae must not differ much among nests irrespective of localities, larger nests have necessarily more vacant cells as shown in Fig. 9.

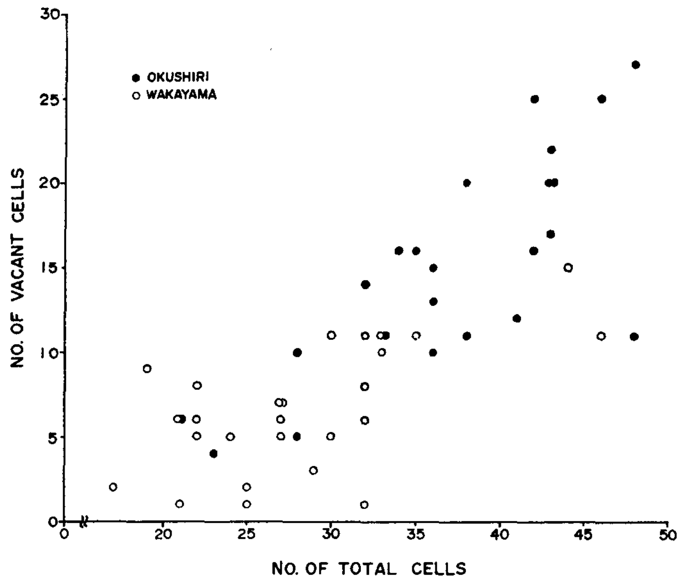

Fig. 9. Relation between the numbers of vacant and total cells nearly at larval appearance in *P. chinensis* in Okushiri and Wakayama.

Closer discussions upon the "vacant cells" is not given for the lack of detailed information upon closely allied species in other regions. But if the "vacant cells" are characteristic to populations inhabiting the cooler climatic regions, it might be advantageous for the regulation of cell temperature together with elongate cells as a *functional envelope* in polistine nests without true envelope surrounding the comb. The comparison of the number of vacant cells is difficult for its fluctuations according to the developmental stages, especially among those obtained at different localities where each population might have proper life modes. Methods to clarify the ecological significances are first, the comparative observations upon the species, especially those belonging to the subgenus *Polistes*, and secondly, the closer studies on a given particular species (*eg. P. chinensis*) as to variations of the number of vacant cells at various localities with special reference to the latitudinal cline of it.

Summary

Two polistine species *P. chinensis antennalis* Pérez and *P. rothneyi iwatai* Vecht, chiefly the former, were observed as to their life cycles at the northernmost limit of their distribution in the Okushiri Island, northern Japan, in June and September, 1970. Some *chinensis* nests were transplanted and reared in Sapporo. Observations revealed the following facts.

1) The nest foundation in *P. chinensis* seemed to occur in late May to early June. In a transplanted nest OI 7027, the first worker emerged in middle July and males and new queens in middle August. Disintegration of nests took place in early to middle September. *P. rothneyi* was observed only in September, but seemed to have the similar life cycle to that of *P. chinensis*.

2) The life cycle in this island is characterized by the shorter nesting period and small colony size. The number of workers was counted for eleven in OI 7027 and the similar size was expected for other nests of this species and also of *P. rothneyi* in the island. This fact suggests the occurrence of the worker, that is, even at the northern limit of their geographical distribution, the presence of the superindividual organization and completion of the life cycles as practiced by temperate populations, inspite of the presence of some modifications due to rigorous climate.

3) In *P. chinensis*, a peculiar habit was seen that the cells located at nest periphery were left vacant in early period of the solitary stage. Such "vacant cells" decreased and disappeared at the time of the first worker emergence.

4) Marked difference of the nest architecture between the Okushiri and southern Japan is the length of cell attained at the end of nesting activity, 25～35 mm in the island, while only 17～25 mm in southern Japan.

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