

LIFE TABLES OF COLONIES AND WORKERS IN A PAPER WASP,
POLISTES CHINENSIS ANTENNALIS,
IN CENTRAL JAPAN (HYMENOPTERA : VESPIDAE)¹

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INTRODUCTION

It is generally accepted that the life table is of great importance in describing and analyzing population dynamics of animals (SOUTHWOOD, 1966; Itô, 1975). In spite of their importance in population problems, however, social insects have mainly been studied in the ethological and sociological aspects since PARDI's pioneering work on the social structure of polygynic association in *Polistes gallicus* (1948). Nevertheless, there are several studies dealing with life tables for social bees and ants (A. D. BRIAN, 1951, 1952; M. V. BRIAN, 1951; MICHENER and WILLE, 1961; BATRA, 1966; FUKUDA and SAKAGAMI, 1968; SAKAGAMI and FUKUDA, 1968; TERADA *et al.*, 1975; SAKAGAMI, 1977; FUKUDA and OHTANI, 1977), but they are confined to a small portion of species and most of them are still imperfect. For the social wasps only fragmentary data are available (*Polistes snelleni*: YAMANE, 1969; *Mischocyttarus drewseni*: JEANNE, 1972; *P. biglumis*: YAMANE and KAWAMICHI, 1975; *P. chinensis antennalis* and *P. jadwigae*: YOSHIKAWA, 1954 and MATSUURA, 1977).

In population studies of social insects, information is required at two levels, i. e., individual and colony, due to their unique mode of life (SAKAGAMI, 1977). Observations are relatively easy in the polistine species, especially those of the genus *Polistes*, for two reasons: First, they make small nests devoid of the outer envelope and they nest in open places, which facilitate direct and close observations on the colony development and intranidal activities. Second, the compartmentalized brood rearing, which is characteristic of all social wasps, enables us to trace individually the births, deaths and other events in the course of brood development.

In this paper life tables are constructed for colonies and workers of *Polistes chinensis antennalis* PÉREZ as the first intentional attempt to study population problems of this species.

MATERIALS AND METHODS

Location

Observations were performed in 1977 in four grassy areas (Fields A-D) located near the west shore of Lake Kitaura (ca. 35°57' N, 140°35' E) in Ibaraki Prefecture.

¹ Contribution No. 49 from Itako Hydrobiological Station, Ibaraki University.

Fields A-C were contiguous each with area of 1570 m², 650 m² and 820 m² respectively. Field D was located about 80 m from the above and had an area of 410 m². These fields had been used for rice after World War II and reclaimed in 1973 for future housing. Nearby were other reclaimed grounds, where scattered houses stood, and rice fields also remained. Predominant plants were *Phragmites communis*, *Imperata cylindrica*, *Miscanthus sinensis*, *Cynodon dactylon*, *Pueraria lobata*, *Artemisia vulgaris* var. *indica*, *Lespedeza cuneata*. Field A was mowed in the autumn of 1976 and the spring of 1977, and the others have been left as intact. Most of the observations were made in Field A and only irregular nest censuses were made in the other three.

Nest census

Nests were usually built very close to the ground on the stems of withered plants, e. g., *Artemisia vulgaris* var. *indica*, *Lespedeza cuneata*, and inside the holes of small concrete blocks piled so as to prevent soil erosion. Nests were censused at irregular intervals (11-22 days) in all fields from April to October. Newly discovered nests were numbered and recorded on a map. In subsequent censuses the following items were checked: (1) total number of cells, (2) number of broods at the most advanced stage and that at the next advanced stage, (3) number of empty cells, (4) presence or absence of the queen, (5) number of adults present, (6) presence or absence of cosmopterigid caterpillars, which eat mainly nest materials and meconia.

The nesting period was divided into five phases according to the brood development and social organization as follows (cf. also Table 1): Phase I, from nest founding by a foundress queen to first hatching of larva, Phase II, from the first hatching to first cocoon spinning, Phase III, from the first spinning to first emergence of worker, Phase IV, from the first emergence of worker to first emergence of reproductive form and Phase V, from the first emergence of reproductive form to disintegration of the colony. Phases I-III correspond with the solitary stage, Phase IV with the superindividual stage and Phase V with the social stage of YOSHIKAWA (1962). The phase of colony development attained by the time of its failure was decided on the bases of the phase recorded at the previous observation, days between it and the last observation when the failure was confirmed, and incubation period of each immature stage. A life table was constructed for colonies using 162 nests out of 187 discovered in the areas. In addition, two other colony survivorship curves, which were obtained by the same way in Funabashi (ca. 35°47' N, 140°3' E, Chiba Pref.) in 1975 and in Kanazawa (ca. 36°34' N, 136°40' E, Ishikawa Pref.) in 1976, are also presented.

Individual census

In order to know precisely the numbers of cells, immatures and infested cells and to trace developmental processes of immatures, cell maps were made for 52 out of 72 nests found in Field A between April 14 and May 1. As a rule nests were mapped once a day until August 13. Thereafter six were selected out of 19 surviving nests, because increased nest size made mapping of all nests impracticable. These six were

divided into two groups and each was mapped every other day. Oviposition, hatching, cocoon spinning, emergence and death of individuals were regarded to have occurred on the day when the events were noted. Newly emerged adults were marked with oil paints without anesthetic and thereafter their intranidal behavior was observed to determine caste (for descriptions of behavior, see MORIMOTO, 1959 and YAMANE, 1970).

RESULTS

1. Colony survival

Developmental processes of two successful colonies (Nests No. 7709 and No. 7749) are summarized in Table 1. Hibernated queens solitarily founded nests from mid April to early May. The first worker emerged in early to mid June. Then the nest

Table 1. Developmental processes in two representative colonies of *Polistes chinensis antennalis* (Itako in 1977).

Stage after YOSHIKAWA (1962)	Phase	Event	No. 7709	Days since discovery	No. 7749	Days since discovery
Solitary	I	Discovery	Apr. 21 (17)	0	Apr. 26 (7+1)	0
		Hatching of first larva	May 5-6 (32+3)	14-15	May 12 (35+3)	16
	II	First cocoon spinning	May 18 (42+1)	27	May 25 (40+1)	29
Superindividual	III	First emergence of worker	Jun. 6 (57+1)	46	Jun. 11-12 (49)	46-47
	IV	First emergence of reproductive	Aug. 7 (529+3)	108	Aug. 7 (278)	103
Social	V	Disappearance of founding queen	Aug. 16-17 (573+2)	117-118	Aug. 29-30 (282+2)	125-126
		Disappearance of brood	Sept. 18-20 (573+2)	150-152	Sept. 24-26 (283+2)	151-153
		Disintegration of colony	Oct. 18 (573+2)	180	Oct. 30 (283+2)	187

(): Number of cells+number of shallow cells insufficient for oviposition.

rapidly grew due to the activities of successively emerging workers. Reproductives (males and/or new queens) first appeared in early August, and they contributed no work to the colony. The nest was not enlarged after mid August, though brood rearing by workers continued for some period. Queens died in mid to late August and the colonies disintegrated between mid August and mid November.

Table 2 presents a life table of colonies using the following parameters: 1) x , represented by five phases of colony development. Phase V was further divided into four subphases, 2) l_x , number of colonies alive at the beginning of each phase, 3) d_x ,

Table 2. A life table for colonies of *Polistes chinensis antennalis* (Itako in 1977).

x	l_x	$d_x F$	d_x	q_x	l_x	d_x'	Lep. (%)
I	162	Unknown	30	18.5	100	18.5	0.0
II	132	Unknown	13	9.8	81.5	8.0	0.8
		<i>Anatrachyntis</i> larvae	1	0.8		0.6	
		Ant(?)	4	3.0		2.5	
		Artifact	1	0.8		0.6	
		Total	19	14.4		11.7	
III	113	Unknown	6	5.3	69.8	3.8	3.5
		<i>Anatrachyntis</i> larvae	2	1.8		1.2	
		Ant(?)	10	8.8		6.2	
		Artifact	2	1.8		1.2	
		Total	20	17.7		12.4	
IV	93	Unknown	4	4.3	57.4	2.5	44.6
		<i>Anatrachyntis</i> larvae	2	2.2		1.2	
		Ant(?)	2	2.2		1.2	
		Artifact	6	6.4		3.7	
		No male production	8	8.5		5.0	
		Rain	2	2.2		1.2	
		Disappearance	2	2.2		1.2	
		Total	26	28.0		16.0	
V(-Aug. 31)	67	Disintegration	6	9.0	41.4	3.7	96.1
V(Sept. 1-30)	61	Disintegration	15	24.6	37.7	9.3	95.7
V(Oct. 1-30)	46	Disintegration	30	65.2	28.4	18.5	94.4
V(Oct. 31-)	16				9.9		

number of colonies failing during each phase, 4) q_x , number of colonies failing per 100 alive at the beginning of each phase, 5) l_x' , relative number alive at the beginning of each phase out of 100 founded, 6) d_x' , relative number failing during each phase out of 100 founded, 7) Lep., relative number of nests infested by larvae of a cosmopterigid moth, *Anatrachyntis* sp.¹, at the end of a given phase to that alive at the beginning of that phase. Figure 1 illustrates a survivorship curve of colonies from Itako in comparison with those from Funabashi and Kanazawa.

Failure rates (q_x , in Table 2) of Phases I to IV ranged from 14.4 to 28.0%. 41.4% of total colonies attained Phase V, that is, succeeded in producing reproductive forms. This value is remarkably high in comparison with those in the other two localities (Funabashi 12.9% and Kanazawa 16.2%, Figure 1). The high failure rate of 28.0% in Phase IV is due to five colonies in Field C which were destroyed by a passing bulldozer and eight which at last produced no males and probably no new queens.

Failure factors were not determined in Phase I. But fifteen out of sixteen colonies in Field A, which were precisely observed by cell maps, contained eggs soon after

¹ Identified by Dr. Hiroshi KUROKO of University of Osaka Prefecture, to whom I express my hearty thanks.

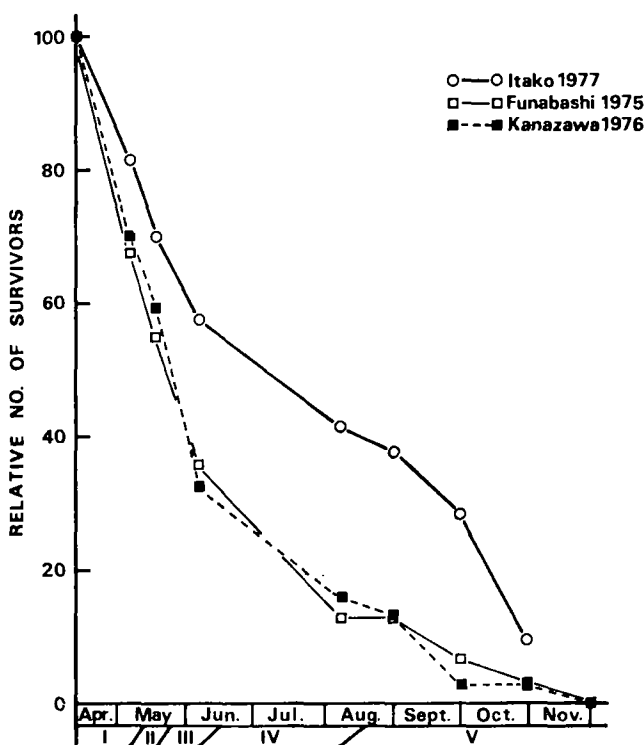


Fig. 1. Comparison of colony survivorship curves of *Polistes chinensis antennalis* in three different localities. I-V: Phases of the colony development, see text P. 70.

queens' disappearance and therefore predation of brood by ants or other predators is ruled out. Presumably they were orphaned by deaths of or abandonment by the queens. Ants (*Lasius niger* and *Pristomyrmex pungens*), artifacts, i. e., destruction by man, and *Anatrachyntis* sp. larvae caused failures of the colonies in Phases II and III. Fourteen colonies (8.6% of total spring nests) were regarded as destroyed by ant attacks, judging from the presence of peculiar small holes on cell walls, although real number of ant-destroyed colonies might be smaller than 14. Some were presumably attacked by ants after the colonies had already failed for other reasons. However, I had the opportunity to observe a critical case in which the queen was able to continue nesting activities, just when I had removed some invading ants. This is sufficient evidence for the fact that the ants are a serious factor of failure during Phases II and III. YOSHIKAWA (1957) also reported an attack by *Pristomyrmex pungens* on a nest of *P. chinensis antennalis*.

Larvae of an *Anatrachyntis* moth began to infest nests in early June (Phases II or III). They seemed to feed mainly on nest materials and meconia and they spun inside the cells. Though I have no direct evidence, they also ate pupae or prepupae (post-defecated larvae) of wasps (see 2. *Brood survival*). But only three colonies

failed by this cause in Phases II and III, so infestation by *Anatrachyntis* larvae is, in most cases, partial and not critical for colony survival. Nineteen colonies whose causes of failure were classified as "Unknown" in Table 2 probably failed by loss of queens, because the nests themselves remained intact, being the same conditions as in Phase I.

Failures in Phase IV were due to *Anatrachyntis* larvae, ants, artifacts, failure in producing the reproductive forms, rains and whole disappearance. Five out of six colonies that suffered artifacts were, as already mentioned, accidentally destroyed at the same time. *Anatrachyntis* larvae had begun to infest at Phases III in case of two abandoned colonies. Colonies which were infested in Phase IV and V were maintained by workers, and larvae were reared in cells other than those occupied by *Anatrachyntis* larvae. Infested nests, however, lost mechanical integrity by encroachment of cell walls, and when they fell to the ground by absorbing rains owing to their remarkably low nest sites (except Field D the mean height was 14.5 cm, n=127, it was 75.1 cm in D, n=11), they were eaten up by woodlice (*Porcellio scaber*). In these cases nesting activities ceased, except that the adults aggregated around the former nest site and the workers continued foraging to feed the new queens and males. Hence, these colonies were not included in failures in Table 2. There was no predation by *Vespa tropica*, which is considered as a major failure factor of polistine colonies after the emergence of workers (MATSUURA, 1977). This species seemed to be scarce in the observation areas, while abundant in a woody terrace situated about 500 m from the fields.

All colonies which attained Phase V were assumed to have disintegrated due to natural termination, judging from external appearances of the nests, though it was possible that *Anatrachyntis* larvae hastened their disintegration.

2. Brood survival

In order to know different patterns of life tables at different periods in a colony cycle, eggs were divided into four groups according to the periods deposited: W1, worker-producing eggs laid between nest founding and first worker emergence, W2, worker-producing eggs laid between the first worker emergence and first deposition of eggs giving rise to reproductive forms, R1, eggs of reproductives laid until first emergence of reproductive form and R2, eggs of reproductives laid from the first emergence of it to termination of nesting activity. Eggs of the reproductives were not separated by sex.

Figure 2 shows daily fluctuation of the oviposition rate in the four periods in Nest No. 7709. It was relatively constant, at about 1.24 eggs/day in Nest No. 7709 or 1.07 in No. 7749 before worker emergence. Thereafter it rose gradually and reached a maximum (59 eggs/day in Nest No. 7709 or 19 in No. 7749) in late July to early August, then declined to zero in mid September. The numbers of eggs laid in each period are shown below the figure.

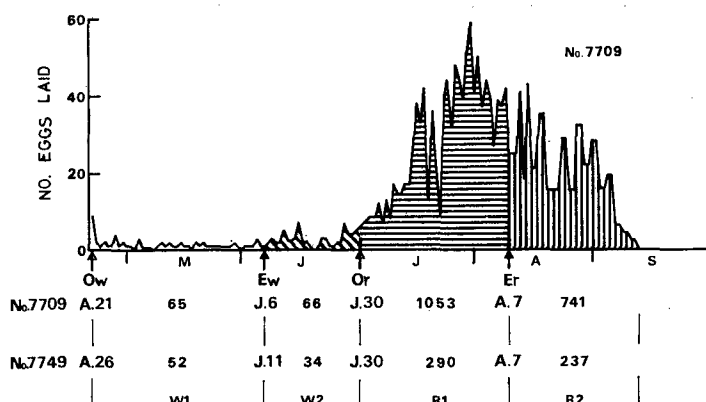


Fig. 2. Daily fluctuation of oviposition in Nest No. 7709, with division of oviposition periods and the numbers of eggs laid during respective periods in Nests No. 7709 and No. 7749. Ow: Start of laying worker-producing eggs, Ew: First emergence of worker, Or: Start of laying eggs for reproductives, Er: First emergence of reproductive, W1: First half of worker-producing eggs, W2: Ditto, second half, R1: First half of eggs producing reproductives, R2: Ditto, second half.

Life tables and survivorship curves for brood are shown separately for the four egg groups in Tables 3 and 4 and Figure 3. In nest No. 7709 the q_x in the egg stage was progressively higher as the period advanced. Values were 21.5%, 34.8%, 59.1% and 95.3% for W1, W2, R1 and R2 respectively. In No. 7749 the figures were essentially the same as in No. 7709 except that the situation of W2 and R1 reversed.

Table 3. Life tables for immature stages in Nest No. 7709.

W1						W2					
x^*	l_x	d_x	q_x	l_x'	d_x'	x^*	l_x	d_x	q_x	l_x'	d_x'
E	65	14	21.5	100	21.5	E	66	23	34.8	100	34.8
L1	51	0	0.0	78.5	0.0	L1	43	0	0.0	65.2	0.0
L2	51	0	0.0	78.5	0.0	L2	43	0	0.0	65.2	0.0
L3	51	0	0.0	78.5	0.0	L3	43	0	0.0	65.2	0.0
L4	51	0	0.0	78.5	0.0	L4	43	0	0.0	65.2	0.0
L5	51	0	0.0	78.5	0.0	L5	43	0	0.0	65.2	0.0
Co	51	2	3.9	78.5	3.1	Co	43	1	2.3	65.2	1.5
Ad	49			75.4		Ad	42			63.7	
R1						R2					
x^*	l_x	d_x	q_x	l_x'	d_x'	x^*	l_x	d_x	q_x	l_x'	d_x'
E	1053	622	59.1	100	59.1	E	741	706	95.3	100	95.3
L1	431	13	3.0	40.9	1.2	L1	35	21	60.0	4.7	2.8
L2	418	14	3.3	39.7	1.3	L2	14	4	28.6	1.9	0.6
L3	404	3	0.7	38.4	0.3	L3	10	3	30.0	1.3	0.4
L4	401	6	1.5	38.1	0.6	L4	7	3	42.9	0.9	0.4
L5	395	42	10.6	37.5	4.0	L5	4	2	50.0	0.5	0.2
Co	353	116	32.9	33.5	11.0	Co	2	2	100.0	0.3	0.3
Ad	237			22.5		Ad	0			0.0	

* E: Egg, L1-L5: 1st-5th larva, Co: Cocoon, Ad: Adult. W1, W2, R1, R2: See text P. 74.

Table 4. Life tables for immature stages in Nest No. 7749.

W1						W2					
x^*	l_x	d_x	q_x	l_x'	d_x'	x^*	l_x	d_x	q_x	l_x'	d_x'
E	52	12	23.1	100	23.1	E	34	17	50.0	100	50.0
L1	40	0	0.0	76.9	0.0	L1	17	0	0.0	50.0	0.0
L2	40	1	2.5	76.9	1.9	L2	17	0	0.0	50.0	0.0
L3	39	1	2.6	75.0	1.9	L3	17	0	0.0	50.0	0.0
L4	38	0	0.0	73.1	0.0	L4	17	0	0.0	50.0	0.0
L5	38	4	10.5	73.1	7.7	L5	17	0	0.0	50.0	0.0
Co	34	2	5.9	65.4	3.9	Co	17	0	0.0	50.0	0.0
Ad	32			61.5		Ad	17			50.0	

R1						R2					
x^*	l_x	d_x	q_x	l_x'	d_x'	x^*	l_x	d_x	q_x	l_x'	d_x'
E	290	59	20.3	100	20.3	E	237	223	94.1	100	94.1
L1	231	14	6.1	79.7	4.9	L1	14	1	7.1	5.9	0.4
L2	217	6	2.8	74.8	2.0	L2	13	5	38.5	5.5	2.1
L3	211	6	2.8	72.8	2.1	L3	8	4	50.0	3.4	1.7
L4	205	2	1.0	70.7	0.7	L4	4	0	0.0	1.7	0.0
L5	203	8	3.9	70.0	2.8	L5	4	0	0.0	1.7	0.0
Co	195	64	32.8	67.2	22.0	Co	4	4	100.0	1.7	1.7
Ad	131			45.2		Ad	0			0.0	

* E: Egg, L1-L5: 1st-5th larva, Co: Cocoon, Ad: Adult. W1, W2, R1, R2: See text P. 74.

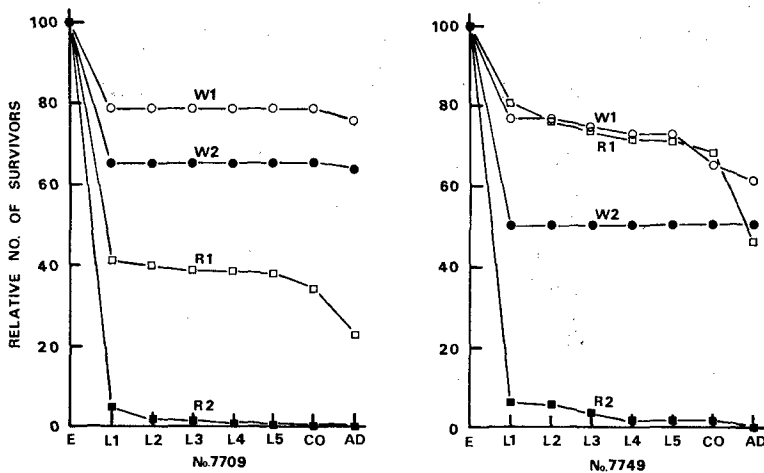


Fig. 3. Survivorship curves of immature stages in two colonies, Nests No. 7709 and No. 7749. E: Egg, L1-L5: 1st-5th larva, CO: Cocoon, AD: Adult. W1, W2, R1, R2: See text P. 74.

Deaths of eggs were phenomenally caused by oophagy by adults. Although the cause of each death was unknown, some possible factors are inferred from the records of cell maps and behavior observations. The main factor for W1 seemed to be nutritive oophagy by the queen. It was probably done to distribute them to newly hatched larvae, judging from indirect evidence that some eggs disappeared soon after

some first larvae hatched. The deaths of R1 and R2 seemed to be non-nutritive oophagy by the queen and workers deriving from their social interaction. Some workers of this species lay eggs even under queenright condition (cf. Table 7), and the frequency of oophagy might relate to the activity level of their oviposition. The egg was often eaten by the egg-layer previous to the deposition of her own egg. The oophagy for R1 took place more often in Nest No. 7709 (59.1%) which produced a greater number of R1 (1053) than in No. 7749 (20.3%) which produced 290 eggs of R1. Indeed oviposition by workers was apparently more frequent in No. 7709 than in No. 7749 (Table 7). But neither interference nor differential egg eating by other individuals (WEST EBERHARD, 1969) was observed when the worker oviposited. Finally, some of R2 might be eaten by males and new queens, which rarely foraged for themselves (see below).

Larval mortality was low through all the oviposition periods (Fig. 3). Mean total d_x' in the larval stage was 3.8 (range: 0-12.5). Deaths in the cocoon stage were also very few (mean d_x' : 1.7, range: 0-3.9) except for R1. High cocoon mortality of R1 (d_x' =11.0 or 22.0) may be attributable to two factors: One is predation by *Anatrachyntis* larvae. Within a few days after cocoon spinning, cocoon cap was broken and the occupant was removed from the cell perhaps by the adult wasp and then the cell was filled by the threads of caterpillars. But it is still uncertain whether the *Anatrachyntis* larvae actually preyed on the wasp's brood. The other is nutritive predation by the reproductives at the end of nesting activity, judging from an appreciably increased mortality of cocooned immatures from mid August onward. Increased number of reproductives and the diminished worker force might result in a reduction of food supply in that period. The reproductive/worker ratio exceeded 1.0 on August 15 in Nest No. 7709 or on August 20 in No. 7749.

3. Adult worker survival

Life tables and survivorship curves are shown in Tables 5 and 6 and Figure 4. It was assumed that an adult was dead when it disappeared from the nest. Females which collected nest materials and/or flesh pellets were regarded as the workers and those without performing these tasks as the new queens.

Survivorship curve of workers is characterized by relatively constant, low mortality (almost $q_x < 10.0$) until the average longevity (ca. 38 days) and somewhat large deaths ($16.7 < q_x < 50.0$) in the subsequent period (Tables 5 and 6). An interesting fact is that there were a few workers that lived two to three times as long as the average longevity. These long-lived workers were the individuals which emerged earlier, performed extranidal tasks for about 30 days, and then stopped foraging and exclusively took charge of intranidal tasks. As already mentioned, these workers laid many eggs in Nest No. 7709. Since their oviposition rates did not differ from that of the queen (Table 7), they are practically regarded as taking a queen's place in the intracolony status. The curve closely resembles that for workers of *Mischocyttarus*

Table 5. A life table for adult workers in Nest No.7709.

x (days)	l_x	d_x	q_x	l_x'	d_x'
0-5	79*	2	2.5	100	2.5
5-10	77	5	6.5	97.5	6.4
10-15	72	6	8.3	91.1	7.6
15-20	66	4	6.1	83.5	5.0
20-25	62	4	6.5	78.5	5.1
25-30	58	5	8.6	73.4	6.3
30-35	53	5	9.4	67.1	6.3
35-40	48	8	16.7	60.8	10.2
40-45	40	10	25.0	50.6	12.6
45-50	30	13	43.3	38.0	16.5
50-55	17	7	41.2	21.5	8.8
55-60	10	5	50.0	12.7	6.4
60-65	5	1	20.0	6.3	1.2
65-70	4	1	25.0	5.1	1.3
70-75	3	0	0.0	3.8	0.0
75-80	3	0	0.0	3.8	0.0
80-85	3	1	33.3	3.8	1.3
85-90	2	0	0.0	2.5	0.0
90-95	2	0	0.0	2.5	0.0
95-100	2	2	100.0	2.5	2.5
100-105	0			0	

Mean longevity=37.8 days.

* The real number emerged was 91, but 12 individuals were excluded since the recognition was impossible for some individuals due to drop-out of markings and the others were died at the marking.

Table 6. A life table for adult workers in Nest No.7749.

x (days)	l_x	d_x	q_x	l_x'	d_x'
0-5	43*	0	0.0	100	0.0
5-10	43	3	7.0	100	7.0
10-15	40	1	2.5	93.0	2.3
15-20	39	4	10.3	90.7	9.3
20-25	35	2	5.7	81.4	4.7
25-30	33	8	24.2	76.7	18.6
30-35	25	1	4.0	58.1	2.3
35-40	24	4	16.7	55.8	9.3
40-45	20	5	25.0	46.5	11.6
45-50	15	7	46.7	34.9	16.3
50-55	8	3	37.5	18.6	7.0
55-60	5	1	20.0	11.6	2.3
60-65	4	1	25.0	9.3	2.3
65-70	3	1	33.3	7.0	2.3
70-75	2	0	0.0	4.7	0.0
75-80	2	0	0.0	4.7	0.0
80-85	2	1	50.0	4.7	2.4
85-90	1	0	0.0	2.3	0.0
90-95	1	0	0.0	2.3	0.0
95-100	1	0	0.0	2.3	0.0
100-105	1	1	100.0	2.3	2.3
105-110	0			0	

Mean longevity=37.8 days.

* The real number was 49.

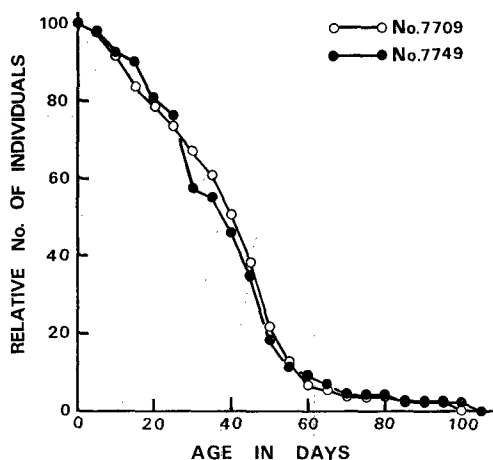


Fig. 4. Survivorship curves of adult workers in two colonies, Nests No. 7709 and No. 7749.

Table 7. Ovipositions directly observed from July 11 to August 15 in Nests No. 7709 (A) and No. 7749 (B).

A							
Individuals	Queen	02	10	Workers*		Others (27 inds.)	Worker total
No. of ovipositions observed	27	22	19	15	12	68	136
B							
Individuals	Queen	02	12	Workers*		Others	Worker total
No. of ovipositions observed	20	1	1	1	1	0	3

* The numerals indicate the individual numbers.

drewseni, especially in respect to occurrence of a few long-lived workers (JEANNE, 1972), though their behavior was not mentioned by him.

4. Worker survival for entire life span

Figure 5 presents survivorship curves of workers for their entire life span (from egg through adult), constructed on the bases of Tables 3-6. Ordinate is relative log number of individuals and abscissa is age expressed by percent deviations from the average longevity. Duration of each immature stage was calculated from the records of 140 individuals (91 in Nest No. 7709 and 49 in No. 7749). Mean duration of each stage was 16 days for eggs, 20 days for larvae and 16 days for cocoons.

The curve is characterized by a distinctly convex shape as that of honeybee workers (SAKAGAMI and FUKUDA, 1968), which is exceptional in insects. However the present pattern is somewhat different from the honeybee pattern in the following

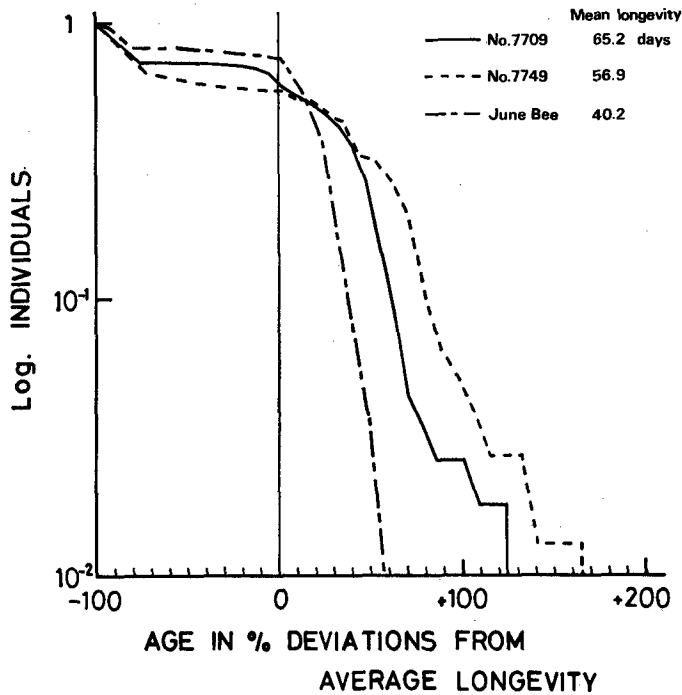


Fig. 5. Survivorship curves of workers for total life span (from egg through adult) in two colonies of *Polistes chinensis antennalis* and that of honeybee (redrawn from SAKAGAMI and FUKUDA, 1968).

points: First, the average longevity is greater (65.2 or 56.9 days vs. 40.2 days), second the mortality in immature stages is higher, and lastly the drop in adult stage starts later and more slowly than in honeybees. The stepwise decline in later period is due to the small sample size, but the occurrence of fairly long-lived workers is remarkable.

DISCUSSION

Colony failure rate in the solitary period (Phases I-III) was remarkably low (42.6%) in comparison with those of other *Polistes* colonies hitherto reported (Table 8 and Fig. 1). The following have been inferred as failure factors in the solitary period by some authors (YOSHIKAWA, 1954; YAMANE, 1969; YAMANE and KAWAMICHI, 1975; MATSUURA, 1977): (1) The loss of the queen either by death due to physiological defect, predation, starvation, adverse weather conditions, or abandonment of the colony by her, (2) Predation of brood by ants, other arthropods, birds or mammals, and (3) Entire loss of the nest by strong winds, rains, artifacts. Especially YOSHIKAWA (1954) attributed the high failure rate of *Polistes* colonies in this period to the evacuation (=loss) of the queen and stressed a conflict between self-maintenance and breeding activity of the queen. Actually, however, most failures due to queen loss are

Table 8. Comparisons of colony failure rate during Phases I-III and Phase IV among *Polistes chinensis antennalis* populations from different localities and among some other species in Japan.

Species	Locality	No. colonies observed	Failure rate (%)		Source
			Phases I-III	Phase IV	
<i>P. chinensis antennalis</i>	Itako (35°57' N, 140°35' E)	162	42.6	28.0	Table 2
<i>P. chinensis antennalis</i>	Kanazawa (36°34' N, 136°40' E)	37	67.6	50.0	Figure 1
<i>P. chinensis antennalis</i>	Funabashi (35°47' N, 140° 3' E)	31	64.5	63.6	Figure 1
<i>P. chinensis antennalis</i>	Tsu (34°43' N, 136°31' E)	264	47.0	40.0	MATSUURA, 1977
<i>P. chinensis antennalis</i>	Tsu (34°43' N, 136°31' E)	157	80.9	50.0	MATSUURA, 1977
<i>P. chinensis antennalis</i>	Ikeda (34°49' N, 135°25' E)	19	84.2	33.3	YOSHIKAWA, 1954
<i>P. biglumis</i>	Oketo (43°40' N, 143°35' E)	40	70.0	8.3	YAMANE & KAWAMICHI, 1975
<i>P. biglumis</i>	Sapporo (43° 3' N, 141°22' E)	23	73.9	50.0	YAMANE & KAWAMICHI, 1975
<i>P. snelleni</i>	Hakken-zan (42°57' N, 141°14' E)	38	84.2	50.0	YAMANE, 1969
<i>P. jadvigae</i>	Wakayama (34°13' N, 135°10' E)	90	53.3	59.5	MATSUURA, 1977

unknown in detail.

In the present case, queen loss, which may nearly correspond with "unknown factors of failure" in Table 2 (column d_xF), affected 30.2% of all spring nests, being lower than in *P. snelleni* and *P. biglumis* (45-74% : YAMANE, 1969 ; YAMANE and KAWAMICHI, 1975). Predation on the brood was less serious than the queen loss, affecting 8.6% of total nests, or 20.3% of total failures in the period. Two species accounted for all of the ant predation. Ants are also important predators on the polistine species in various localities, especially in lower latitudes (YOSHIKAWA, 1954; JEANNE, 1975 ; YAMANE pers. com.). On the other hand, in a certain district of northern Japan, foxes (*Vulpes vulpes schrencki*), which extinguished more than 25.0% of solitary nests, are one of the most serious predators, while ants are practically negligible there (YAMANE and KAWAMICHI, 1975).

Consequently, relatively low rates of queen loss and brood predation compared with those in other populations and species would be principal causes of high colony survival during the solitary stage, although queen loss was the most serious cause of failure in this population. Two factors may be responsible for the low rates of queen loss and brood predation. First, these areas were reclaimed from rice fields about four years ago and the habitat might contain fewer species of predators on the queen and the brood. When a species invades a new habitat, it is often the case that its predators do not arrive until later. Second, food for the brood appeared to be abundant. I frequently observed that queens (and also workers) were preying on adults of

chironomids (*Orthocladius akamusi* and some other species) which emerged in enormous numbers from Lake Kitaura.

After the emergence of workers, colony failure rate was lower (28.0% in Phase IV, see Table 8). Predation by *Vespa tropica*, birds and mammals, and interference by man have been regarded as causes of failure in this period (SAKAGAMI and FUKUSHIMA, 1957; JEANNE, 1975; MATSUURA, 1977). *V. tropica* may play a significant role in controlling polistine populations in Asia. Ant attacks are also serious threats for tropical populations as in the solitary stage, but for the temperate populations they may have minor importance as predators.

Major failure factors in Phase IV were failure to produce sexuals (5.0% of total colonies, or 30.8% of total failures in the period) and artifacts (3.7% or 23.1%) in the present study. Failure in producing the sexuals seems to have arisen from physiological inferiority of the queens, but the details are not clear for the lack of precise observations. Human interference seems to have been lower in the fields than in the case nested under the eaves and rafters of houses, because the fields were mostly isolated by fences. It is noteworthy that there was no predation by *V. tropica*.

It has been stressed that in social insects colony failure rate is the highest in the solitary period. WEST EBERHARD (1975) discussed the evolution of non-solitary nest foundation, i. e., polygyny and swarming, in connection with the high vulnerability of nests in this period. In the present study 69 (42.6%) out of 162 nests failed in the solitary period (Phases I-III) and 26 (28.0%) in Phase IV, which lasted a little longer than the preceding three phases combined (Table 1). There was almost no external failure factor in Phase V, hence it may be concluded that the solitary period is the most critical one for the survival of colonies. But this is not always the case with other studies (Table 8). Namely failure rate in the solitary stage is not so drastically high in some cases, although there is a possibility of underestimation due to the time lag between colony foundation and discovery by observer. Colony failure rate and factors are highly variable by different local environments, e. g., the presence or absence of *V. tropica*, predatory ants, birds and mammals, and abundance of available food. Especially in the area where *V. tropica* occurs or interference by man is severe, colonies may suffer high risk of destruction even after the worker emergence.

Average mortality of worker brood was around 35%, being very low among insects but not so different from the mortality level of solitary nest-building wasps and bees (40-60% : IWATA, 1953 ; OHGUSHI, 1955 ; DANKS, 1971 ; FREEMAN, 1973 ; FREEMAN and TAFFE, 1974 ; TAFFE and ITTYEPE, 1976). It is notable that nearly all deaths (85.7%) in the egg stage are considered to be caused from cannibalism by adults, or at least, not from predation or parasitism by external enemies, while these are main mortality factors in solitary species. Further deaths frequently take place in the larval and pupal stages as well as in the egg stage in the solitary species. The deaths of the brood of reproductives concentrated on the egg stage. As already

mentioned, the high egg mortality is probably related to active oviposition by workers and the subsequent oophagy. The active worker oviposition is interpreted in two different ways: First, the workers can lay eggs by incomplete queen control due to imperfect caste differentiation. Second, it is a secondary derivative during social evolution (i. e., production of nutritive eggs or production of males by workers, cf. SAKAGAMI *et al.*, 1973). Taking account of the rather large colony size of this species among the *Polistes* and other peculiar bionomic features (e. g., presence of peripheral vacant cells, etc.), I consider the second interpretation more probable. But, for the time being, the available data are not conclusive.

In any case possible mortality factor is cannibalism by adults, i. e., nutritive oophagy by the queen, oophagy by the queen and workers previous to their oviposition, and cannibalism by reproductive forms, except for possible predation by *Anatrachyntis* larvae in later nesting period. FUKUDA and SAKAGAMI (1968) stressed the self-control of population by egg eating in honeybee colony. MATSUUA (1973) also claimed that deaths of immatures were almost entirely caused from the cannibalism by adults in *Vespa crabro flavofasciata*. As various predators and parasitoids for immatures have been known in many social wasps (RABB, 1960; NELSON, 1968; SPRADBURY, 1973), social wasps cannot exclude completely external factors of mortality from immatures. But it may be concluded that in social wasps intracolony factors play far more important roles in immature mortality than do extracolony ones. MATSUURA (1977) considered that the cannibalism in polistine and vespine wasps is performed as a kind of feedback system of the proteinaceous nutrients, and that it may substitute for food storage habit in bees. Cannibalism, operating as nutrition regulating mechanism, is also observed in the Coleoptera (HO and DAWSON, 1966). The cannibalism in the present species seems not to be explained only as a food regulation mechanism but to have much more relation to the social organization (e. g., worker oviposition). But the observations are insufficient to give a conclusion.

In contrast to workers of highly eusocial bees, which have an temporal polyethism, workers of social wasps have no distinct polyethism among them. Such a difference in behavior is reflected on the shape of survivorship curve, as TERADA *et al.* (1975) suggested. That is, workers of honeybee and stingless bee (*Plebeia droryana*) enjoy very low mortality during first 20-25 days of a household period (SAKAGAMI and FUKUDA, 1968; TERADA *et al.*, 1975), while in *P. chinensis antennalis* the mortality of that period is higher (Fig. 4), since the workers can start extranidal activities a few days after the emergence. Occurrence of some long-lived workers is another remarkable feature of *P. chinensis antennalis*. This is perhaps due to the fact that these individuals practically stopped external activities in the second half of their life, and it is completely different from the pattern of polyethism in the honeybee and in the stingless bee. This type of survivorship curve is also reported in a social wasp, *Mischocyttarus drewseni* (JEANNE, 1972). Survivorship curve of the workers for entire

life span (from egg through adult) is characterized by a distinctly convex shape. Although it is not much the same as in honeybee workers and man, it is probably exceptional among insects. Comparing the survivorship curves of various insects, ITÔ (1959) concluded that increased parental care generally decreases the juvenile mortality, and the present result supports his assertion to some extent. Relatively high mortality of the eggs is inconsistent with the opinion of ITÔ. But it must be taken into account that at least a part of the cannibalism might serve as food regulating mechanism as MATSUURA (1977) suggested. If so, high egg mortality should not be regarded as a simple result of insufficient maternal care.

Finally the difficulties to compare the survivorship curves of social insects with those of non-social insects are referred to. Since the workers themselves don't reproduce offspring, they are in a sense regarded as somatic extensions of the queen (WILSON, 1971)¹, the survivorship curves of the reproductive females, i.e., queens, must be prepared for valid comparisons among various species. However, it is difficult to obtain the survivorship curves of adult queens, since for the time being we have no effective method to know the mortality rate between dispersal from the mother nest in autumn and start of colony foundation in the next spring. Even concerning the immature stages some difficulties are present: The eggs laid by the queen cannot be distinguished from those laid by workers and to know the sexes at the egg and larval stages is practically impossible.

SUMMARY

A paper wasp *Polistes chinensis antennalis* PÉREZ was observed in Itako (ca. 35°57' N, 140°35' E), Ibaraki Pref., Japan, from April to October in 1977, for the purpose of constructing life tables at colony and individual levels. The results obtained are as follows:

(1) Out of 162 colonies founded in spring by hibernated queens, 93 ones (57.4%) survived through the solitary nesting period and 67 ones (41.4%) produced sexual forms. Hence it is concluded that the solitary stage is the most critical period for the survival of the colony in this population. But the survival rate in the solitary stage was remarkably higher than those hitherto reported in *Polistes* wasps. Some possible reasons were referred to concerning the higher value.

(2) Eggs were divided into four groups according to the periods when they were laid. Brood mortality increased in order of the periods and finally reached 100% for the fourth group. The major mortality factors were cannibalism by adults and probable predation by larvae of a cosmopterygid moth, *Anatrachyntis* sp. Intracolony factors seem to play the most important role for the immature mortality, but it remains open whether the cannibalism plays a role in the regulation of intracolony population.

¹ In the case of the present species, however, frequent oviposition by workers makes the problem more complicated. This remains as a future subject to be clarified.

(3) Worker oviposition was common even under the queenright condition. It was extremely frequent in Nest No. 7709 and this seems to have activated the egg-eating activity and increased the egg mortality of the brood of reproductives.

(4) Adult workers showed a convex survivorship curve, with an average longevity of 37.8 days. Comparing with the survival patterns of honeybee and stingless bee (*Plebeia droryana*), it is noteworthy that they did not have an initial extremely high survival period, but had a few long-lived workers which frequently laid eggs.

(5) Survivorship curve of workers for their entire life span (from egg through adult) was distinctly convex and it is similar in major features to that of honeybee workers. The result seems to support Itô's (1959) assertion to some extent that the types of survivorship curves correlate with the degree of evolution in the maternal care on the broods.

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中部日本におけるフタモンアシナガバチの巣および働き蜂の生命表

宮野伸也

巣および働き蜂の生命表を作製するため、1977年4月から10月にわたり、茨城県潮来町（約35°57' N, 140°35' E）でフタモンアシナガバチ *Polistes chinensis antennalis* Pérez の観察を行ない、以下の結果を得た。

- (1) 春に越冬女王により創設された162巣のうち、93巣（57.4%）が単独営巣期を生き残り、さらに67巣（41.4%）が次世代成虫を産出した。この結果から、この地域個体群にとっては、単独営巣期がその生存にとって最も危険な時期であることを結論した。しかし、アシナガバチ属におけるこれまでの報告に比べ、単独営巣期の生存率はかなり高く、これについていくつかの理由が推定された。
- (2) 産卵時期によって、卵を4つのグループに分けた。非成虫期の死亡率は、この順で大きくなり、最後のグループでは100%に達した。主な死亡要因は、成虫によるともぐいであり、他にトガリホソガ科の *Anatrachyntis* sp. 幼虫による捕食が推定された。非成虫期の死亡については、コロニー内の要因が最も重要であると思われるが、ともぐいがコロニー内の個体数調節に関与しているかどうかは不明である。
- (3) 女王の健在な巣での働き蜂による産卵は、きわめて普通であり、特に No. 7709 の巣では頻繁に行なわれ、これが活発な卵食を誘発し、生殖個体の卵期死亡率を増加させたものと思われる。
- (4) 働き蜂の成虫期の生存曲線は凸型を示し、その平均寿命は37.8日であった。ミツバチやハリナシバチに比べ、初期の生存率の高い時期がないこと、および数匹の特に長命な個体が生じることが特徴的であった。
- (5) 卵期から成虫期を含めた全発育期間を通じての働き蜂の生存曲線は、明瞭な凸型を示し、概略において、ミツバチの働き蜂のそれと似たものであった。この結果は、生存曲線の型と母虫による育児行動の進化の程度に関する伊藤（1959）の論議をある程度支持するものと思われる。