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COLONY DEVELOPMENT, WORKER BEHAVIOR AND MALE PRODUCTION IN ORPHAN COLONIES OF A JAPANESE PAPER WASP, *POLISTES CHINENSIS ANTENNALIS* PÉREZ (HYMENOPTERA: VESPIDAE)[1]

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Introduction

In those social wasps and bees in which colonies are founded by a single queen alone (haplometrotic independent founding), loss of the queen before the first emergence of worker usually leads to colony extermination. When the queen is lost after or just before worker emergence, however, first brood workers often continue nesting activities. Rau (1929) called such a nest 'orphan' and reported oviposition by workers in some polistine species. There have been several short term studies of social relations between workers left in the nest (Pardi, 1948; Free, 1955; Morimoto, 1961a, b; Landolt et al., 1977), but so far none of the ultimate fate of the orphan colonies.

In previous papers (Miyano, 1980, 1983), I presented population ecological information about *Polistes chinensis antennalis* Pérez obtained from population-wide colony censuses and observations of normal colonies[2]. In the present paper I describe colony development, worker behavior, the number of males, and some other population ecological properties of orphan colonies of the same species, and discuss the production system of the next generation of this species.

Materials and Methods

Observations were carried out in four grass fields (A–D) located at Itako, central Japan, in 1977 (see Miyano, 1980 for details of the habitat).

All *P. c. antennalis* colonies discovered in Fields A–D were checked at 11–22 day intervals from April 14 to October 30 for the following points: (1) whether the nest is active or abandoned, (2) presence or absence of the queen and (3) total number of cells.

The development of 52 selected colonies in Field A was recorded in greater detail by means of nest maps. Out of these, two were orphaned after the emergence of a few

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[1] Contribution no. 68 from Itako Hydrobiological Station, Ibaraki University.

[2] Normal colonies designate those in which the founding queens exist until early August and hence which have already received eggs of reproductives.

workers. They were, as a rule, mapped once a day from April 24 to August 13 (colony no. 7742) or July 25 (colony no. 7744), and thereafter every second day until October 30. Newly emerged wasps (up to 2 days old) were taken from the nest without anesthesia, weighed on a microbalance to the nearest 0.1 mg, marked individually with oil paints, and put back on the nest. Oviposition, hatching, cocoon spinning, emergence, and death of individuals were treated as having occurred the day they were recorded on nest maps.

Worker behavior was observed on June 14 (9.6 h), June 28 (2.5 h), July 15 (2 h) and August 4 (2 h) after the queen's disappearance in colony no. 7742. Recorded in these were dominance interactions, loads brought in by foraging workers, food exchange between workers, and oviposition.

RESULTS

1. Incidence and size of orphan colonies

Of 81 colonies active in early August, 20 (24.7%) were orphan colonies (Table 1). Percentage of orphan colonies varied from 16.7 to 28.6 among the four fields. The gross average size of orphaned nests was about 3/4 that of the normals.

2. Development of two orphan colonies

Two colonies (no. 7742 and no. 7744) developed normally with no sign of parasitism,

Table 1. Numbers and nest size (number of cells) of orphan and normal colonies in four observation fields in early August.

Field	Orphan Colonies			Normal Colonies		
	No. of Colonies (%)	Nest size		No. of Colonies (%)	Nest size	
		Mean	Range		Mean	Range
A	12(28.6)	155.3	73-ca.220	30(71.4)	242.6	69-575
B	4(18.2)	198.0	ca.140-252	18(81.8)	216.3	88-ca.400
C	3(27.3)	166.7	ca.140-ca.180	8(72.7)	239.4	76-ca.350
D	1(16.7)	210		5(83.3)	180.8	ca.120-ca.300
Total	20(24.7)	168.3	73-252	61(75.3)	229.4	69-575

Table 2. Composition of two colonies of *P.c. antennalis* at the time of the queen's disappearance.

	Colony	
	no. 7742	no. 7744
Date	June 12	June 26
No. cells	42	41
No. eggs	9	17
No. larvae	16	17
No. cocoons	8	5
No. empty cells	9	2
No. workers	4	5

while their queens were present. The queens disappeared on June 12 from no. 7742 and on June 26 from no. 7744, due to unknown cause(s). Table 2 shows the colony composition of each just after the queen's disappearance. The eldest worker was 6 days old in no. 7742 and 14 days old in no. 7744, and probably begun foraging.

In colony no. 7742 new cell construction stopped for 15 days after the queen's disappearance and then the number of cells increased rapidly and finally reached 183 (Fig. 1). In colony no. 7744 new cell construction almost ceased during the 14 days before the orphaning. It resumed 5 days after the disappearance and the number of cells finally attained 177 (Fig. 1).

Worker oviposition was first noted two days after the queen's disappearance in no. 7742 and 5 days in no. 7744. At least 534 (no. 7742) and 366 (no. 7744) eggs were laid by workers. These figures are minimum estimates, because some eggs were probably cannibalized by adults before being recorded.

The total brood in each nest reached a maximum of about 170 in early August, then rapidly declined to zero in early September. The number of eggs peaked first, followed by larvae and cocoons. Eggs had a second peak a little lower than (no. 7742) or as high as (no. 7744) the first one (Fig. 1).

In no. 7742 males began to emerge on July 31, four days after the emergence of the last female, and the last male emerged on August 25 (Fig. 2). In no. 7744, on the other hand, there was some overlap between emergence of females and males (Fig. 2): the last female emerged on August 12, and males emerged between August 6 and September 2 or 3. The nest maps show that all females of each colony came from eggs laid by the

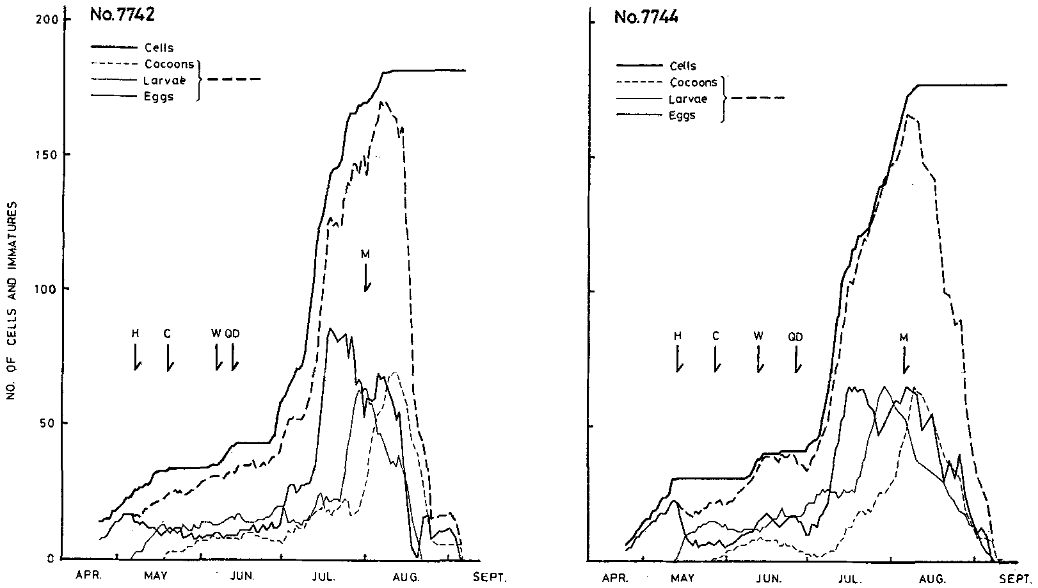
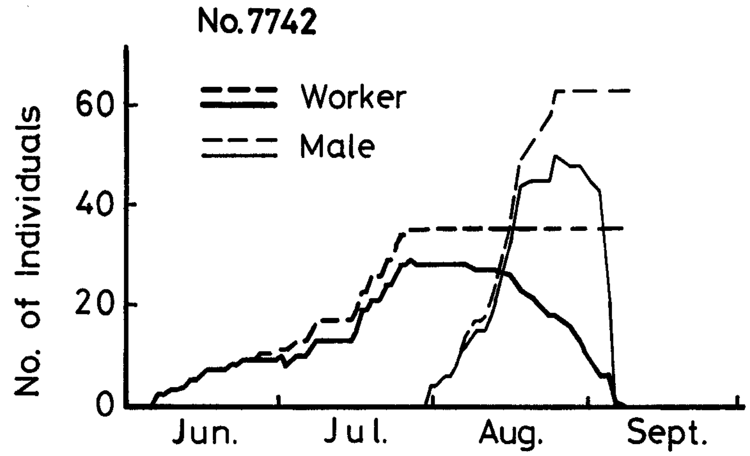


Fig. 1. Changes in numbers of cells and immatures in two orphan colonies. H: Hatching of first larva, C: Spinning of first cocoon, W: Emergence of first worker, QD: Queen's disappearance, M: Emergence of first male.



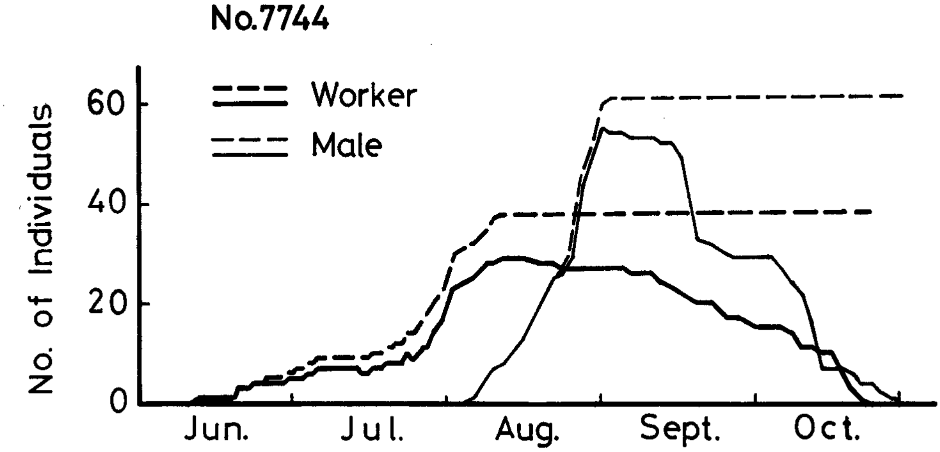


Fig. 2. Changes in numbers of workers and males (solid lines) and the cumulative curves (dashed lines) in two orphan colonies.

queen. On the other hand, all males came from eggs laid by workers after the queen's disappearance.

3. Worker behavior

A linear dominance-hierarchy was established among workers of no. 7742 on the 2nd day after the queen's disappearance (Table 3). The dominance order was consistent with the order of emergence (worker age). The dominant worker antennated the head or thorax of the subordinate worker and sometimes bit its antennae, legs, and wings. The subordinate took a motionless posture and pulled in its antennae and legs. Dominance interactions occurred 26.9 times per hour on the 2nd day after the disappearance, peaked in the 16th day (58/h) then gradually decreased (22/h on 33rd day and 5.5/h on 53rd day), although the number of workers increased during this period. The top-dominant worker most frequently exerted dominations upon the next-ranked worker on the 2nd

Table 3. Number of dominance interactions among pairs of workers and number of ovipositions in colony no. 7742. Based on 9.6 h of observation on June 14 (2 days after the queen's disappearance).

Dominant worker	Age (Days)	Subordinate worker					Total dominations	Ovipositions
		W_2	W_1	W_3	W_4	W_5		
W_2	8	—	159	50	0	0	209	2
W_1	8	0	—	34	11	2	47	0
W_3	5-6	0	0	—	1	0	1	0
W_4	2-3	0	0	0	—	1	1	0
W_5	1	0	0	0	0	—	0	0
Total submissions		0	159	84	12	3	258	Total 2

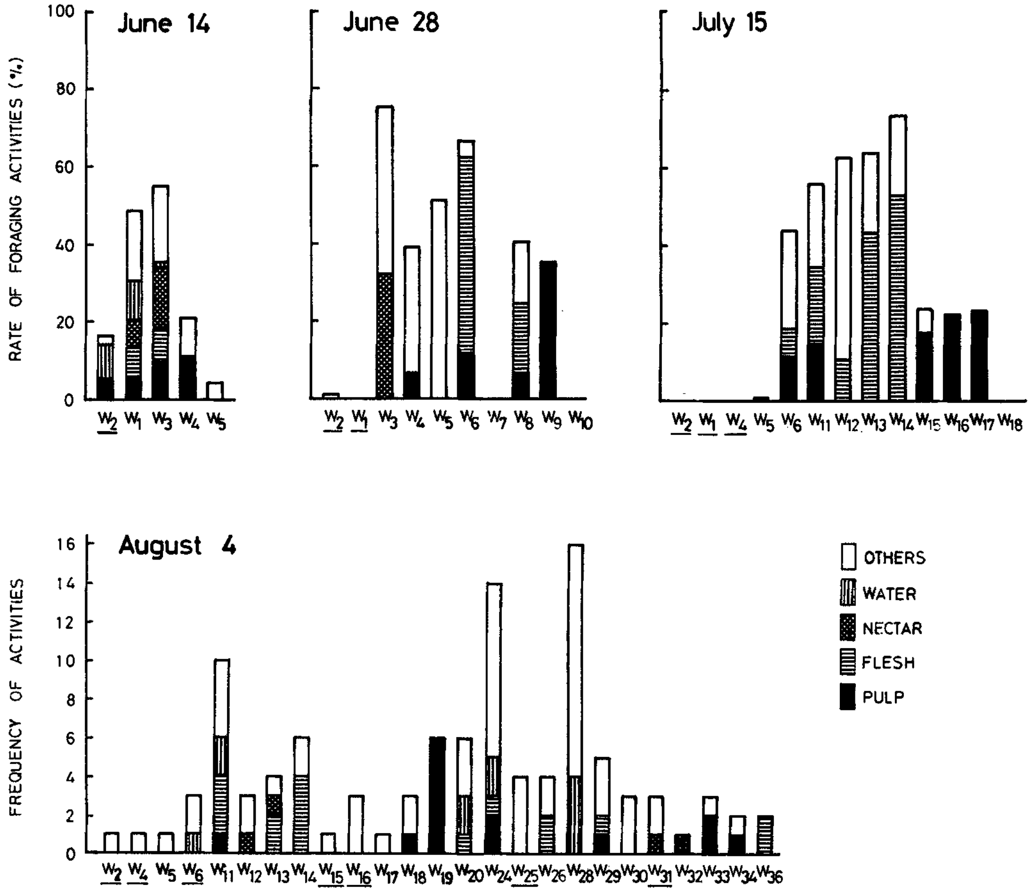


Fig. 3. Comparison of foraging activities of individual workers in colony no. 7742. Based on 9.6 h of observation on June 14 (2 days after the queen's disappearance), 2.5 h on June 28 (16), 2 h on July 15 (33), and 2 h on August 4 (53), respectively. W_1–W_{36} mean codes of workers. Underlined individuals laid eggs during the observation.

Table 4. Number of ovipositions recorded by direct observation in colony no. 7742.

Date	Workers								Total
	W_2	W_1	W_4	W_5	W_6	W_{15}	W_{16}	7 others	
Jun. 12–Jul. 30	14	11	10	1	2	3	2	3	46
Jul. 31–Sept. 3	8	2	6	3	11	6	4	5	45
Total	22	13	16	4	13	9	6	8	91

and the 16th days.

Except on the 2nd day, multiple workers laid eggs and the number of egg-layers gradually increased throughout four observations (Fig. 3). Egg-layers were the dominant workers except on the 53rd day, when dominance interactions were infrequent and some individuals not involved in dominance interactions also laid eggs. Table 4 summarizes the directly observed ovipositions, showing the existence of multiple egg-layers.

Reproductive competition among workers was seen in physical interference with each others' egg-laying and in eating each others' eggs, as illustrated in the following observations. On the 16th day after the queen's disappearance there were two egg-layers, W_2 (top-dominant) and W_1 (second-dominant), each laid two eggs. Before its second oviposition W_2 ate the first egg of W_1. W_1 ate two eggs laid by W_2. When W_1 proved a cell with the tip of abdomen, in preparation for laying an egg, she was strongly attacked by W_2 by antennal crashing and biting, so that she withdrew her abdomen from the cell. After this W_1 proved cells 12 more times without laying. In 10 of these W_1 was furiously attacked by W_2. On the 14th attempt W_1 succeeded in laying an egg while W_2 was on the opposite side of the comb.

On the 33rd day after the queen's disappearance, W_2, W_1, and W_4 (hierarchy in this order) competed for egg-laying. W_2 laid two eggs, and preceding the second oviposition she ate an egg of W_4. W_1 laid an egg and ate one of W_4' eggs. W_4 laid 3 eggs, all of which were eaten, while she ate no eggs. No physical interference of egg-laying was observed during these ovipositions.

Most extranidal activities were performed by subordinates; dominants scarcely left the nest (Fig. 3). However, some workers (W_6, W_{26}, and W_{31}) performed both foraging and egg-laying on the 53rd day after the queen's disappearance (Fig. 3).

Table 5. Direction of flow of flesh and nectar between workers of known dominance rank in colony no. 7742. In each case the first number (before the slash) represents food transferred from a lower-ranked to a higher-ranked worker, while the second number represents a transfer in the opposite direction.

	Date			Total
	June 14	June 28	July 15	
Observation time (hours)	9.6	2.5	2.0	14.1
Transfer of flesh	4/10	2/1	1/1	7/12
Transfer of nectar	4/5	1/1	0/0	5/6

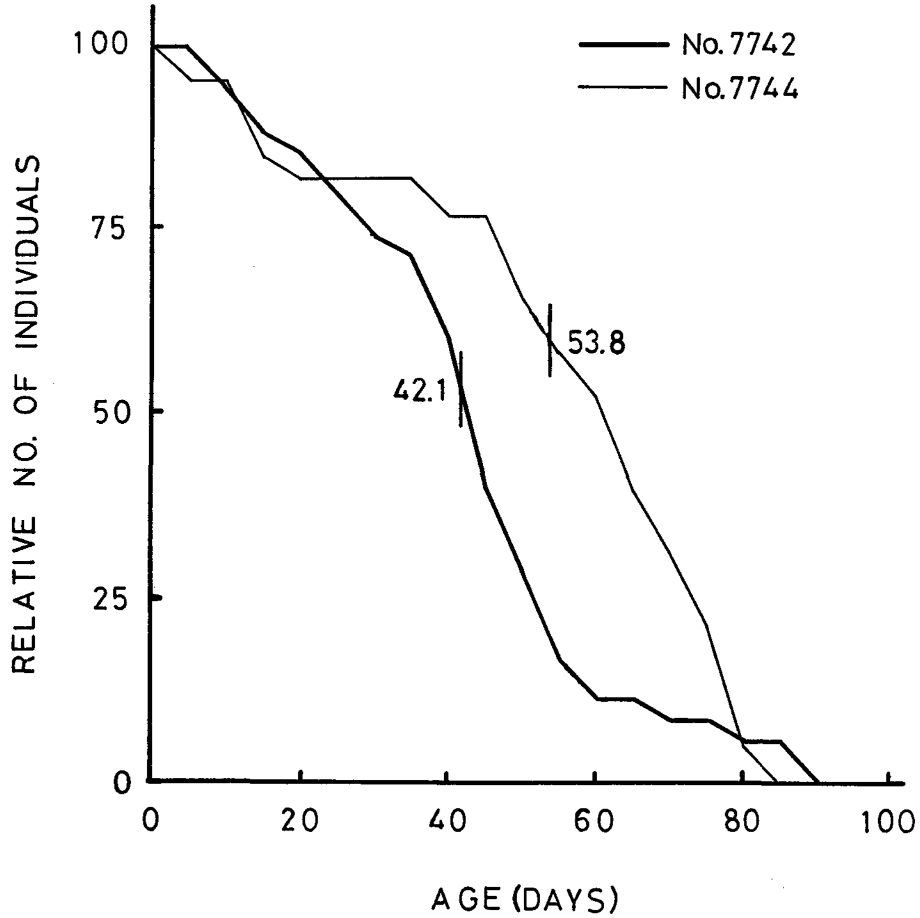


Fig. 4. Survivorship curves of adult workers in two orphan colonies. Numerals in figure show mean longevity.

There was no tendency for a net flow of nutrients to dominant workers (Table 5). On one occasion on July 15, W_6 offered a flesh pellet she foraged to nest mates by pushing it against the mouth of the donee, but no one willingly received it. After a 50 seconds of unsuccessful attempts, W_6 began to masticate the pellet and finally fed it to larvae herself.

4. Survival pattern of workers in the nest

Fig. 4 shows the survivorship curves of adult workers with disappeared individuals presumed dead. Four long-lived workers (W_1, W_2, W_4, and W_5) of colony no. 7742, which emerged earliest and survived more than 60 days, retained high rank and were proficient egg-layers. In no. 7744, twelve out of 15 workers which emerged in August survived more than 60 days.

5. Brood survival

Brood survivals were compared among 4 groups: (1) the entire worker brood laid by the queen (W), (2) that part of worker brood which was still immature at the time of

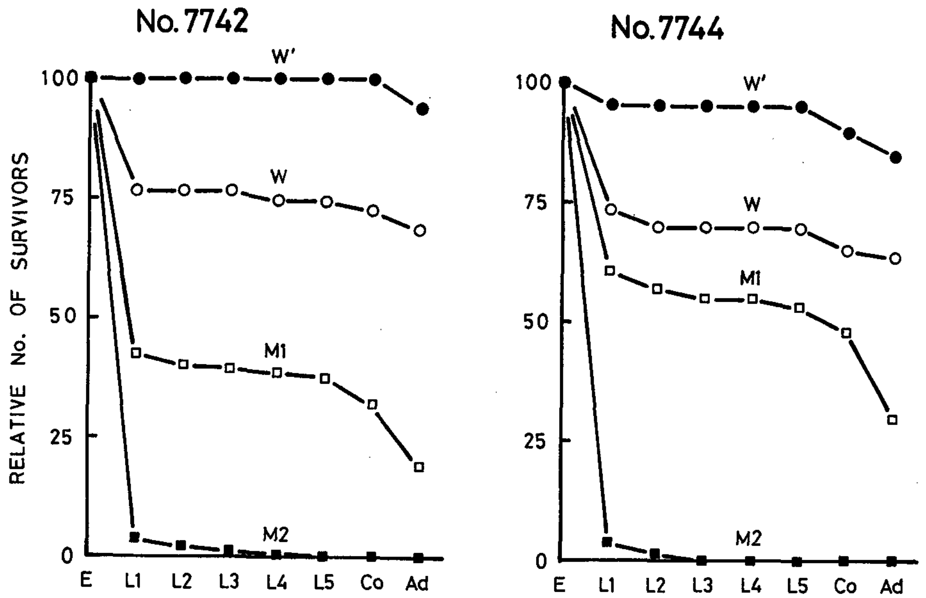


Fig. 5. Survivorship curves of immatures in two orphan colonies. E: Egg, L1–L5: First to fifth larva, Co: Cocoon, AD: Adult. W', W, M1 and M2: See text P. 353.

the queen's disappearance (W', cf. Table 2), (3) early male brood laid by workers from the time of the queen's disappearance to the emergence of the first male (M1), and (4) late male brood laid by workers after the emergence of the first male. Numbers of eggs for W, W', M1, and M2 were 51, 33, 326, and 208 respectively in no. 7742 and 63, 39, 202, and 164 respectively in no. 7744.

Survival rates of W during immature stages were 68.6% for no. 7742 and 60.4% for no. 7744 (Fig. 5). The mortality was highest (ca. 25%) at the egg stage and low (0–8% of first eggs) at the larval and cocoon stages. Survival rates of W' were remarkably high (93.9% for no. 7742 and 84.6% for no. 7744), indicating that workers did not cannibalize W'.

High egg mortalities for M1 (ca. 60% for no. 7742 and ca. 40% for no. 7744, Fig. 5) and M2 (ca. 95% for both) arose from mutual oophagies among egg-layers. Egg mortalities of M1 and M2 are underestimates, because egg eating occurrred so soon (within 10–80 min) after oviposition that more eggs must have been laid than recorded. Mortality rates of the 5th instar larvae and cocoons of M1 were higher than W and W' (Fig. 5). Most deaths (52 out of 63) occurred after August 16 in no. 7742 and all (46) did after August 10 in no. 7744. They were presumably due to cannibalism by adults or attacks by larvae of an *Anatrachyntis* moth (which were seen in nests on August 10–11). Brood of M2 were almost entirely cannibalized by adults at the egg stage and produced no adults (Fig. 5).

6. Productivity

Thirty five and 38 females were produced from eggs laid by the queen in no. 7742 and no. 7744, respectively. I have treated all as workers, because most of them foraged.

Table 6. Numbers and average live-weights (mg) of adults produced and number of cells constructed in two orphan and two normal colonies of *P.c. antennalis*.

Colony	no. 7742	no. 7744	no. 7709[1)]	no. 7749[1)]
Condition	orphan	orphan	normal	normal
Worker				
a) Number	35	38	91	49
b) Average live-wt.	85.4	87.8	96.2	109.6
SD, *n*	12.7, 33	17.4, 38	18.1, 90	18.8, 48
New queens				
c) Number (c/a)	0(0)	0(0)	104(1.14)	100(2.04)
d) Average live-wt.			136.4	148.1
SD, *n*			10.7, 104	11.3, 98
Males				
e) Number (e/a)	63(1.80)	61(1.61)	133(1.46)	31(0.63)
f) Average live-wt.	80.4	71.6	79.7	76.8
SD, *n*	10.7, 63	6.8, 60	9.1, 133	9.3, 31
Cells				
g) Number (g/a)	182(5.20)	177(4.66)	575(6.32)	285(5.82)

[1)] after Miyano, 1983

Two orphan colonies produced a number of male comparable to normal colonies, as reported by Miyano (1983), while they produced a smaller number of cells and no new queens (Table 6). Taking new queens and males together, the two orphan colonies were about 1/3 as productive as the two normal colonies in numbers of reproductives. More importantly, the orphan colonies were only 22% as productive in total mass of reproductives (5.07 and 4.37 g, compared with 24.79 and 17.19 g).

A single worker of orphan colonies raised about 2/3 as many reproductives as normal ones (1.80 and 1.61 vs. 2.60 and 2.67). If the productivity per worker is expressed in terms of body weight, 1.72 mg males/mg worker was produced in no. 7742 and 1.31 mg males/mg worker in no. 7744. These figures were about a half of those of two normal colonies (2.85 and 3.19 mg reproductives/mg worker, Miyano, 1983).

The average live-weight of workers was significantly less in the orphan colonies than the normal ones ($t=5.35$, df$=207$, $P<0.001$). The average live-weights of males, on the other hand, were nearly the same.

Discussion

It seems common in the social wasps and bees that there appear laying workers when the queen is lost (*Polistes*: Yamanaka, 1928, Pardi, 1948, Morimoto, 1954, Yoshikawa, 1956, Metcalf and Whitt, 1977, Strassmann, 1981b; *Mischocyttarus*: Litte, 1977; *Vespa*: Ishay et al., 1965, Yamane, 1974; *Vespula*: Shida, 1959, Landolt et al., 1977; *Bombus*: Free, 1955, Hobbs, 1965, Sakagami, 1976). Even in the honeybees, one of the most advanced social Hymenoptera, workers begin to lay eggs after dequeening (Sakagami, 1958). In the case of the honeybees, however, orphan colonies sooner or later lose colonial organization and become extinct, so that egg-laying by workers has little genetic significance.

The present study shows that in *Polistes chinensis antennalis* orphan colonies are successfully carried on by workers and can significantly contribute to the next generation by producing male offspring. SUZUKI (1981a) reported 119–337 (mean 244.7) cells as the final colony size in normal colonies and the colonies produced 21–136 (mean 57.9) males and 22–98 (mean 48.3) new queens. Smaller colony size (average 168.3 cells) and lower productivity (about 60 males) in orphan colonies are mainly due to the limited worker force. The upper limit on the worker force is determined by the numbers of workers and brood present at the time of the queen's disappearance. Besides this, worker efficiency is also reduced (Table 6). Occurrence of multiple egg-layers lessens the number of foragers and increases the social conflicts, which increases the mortality of eggs. The high frequency of orphan colonies (27.4%) indicates that the number of orphan-produced males is not trivial at the population level. Twenty six percent of reproducing colonies of *P. metricus* (METCALF, 1980) and 3% of *P. fuscatus* (NOONAN, 1981) are reported to be orphan.

Violent dominance-subordination interactions are a marked feature of orphan colonies. The eldest worker, occupying the top rank, left the nest rarely and laid eggs, behaving much like the legitimate queen of the normal colonies. But she could not monopolize oviposition. Probably a smaller physiological gap among workers than that between the queen and workers evoked intense conflicts which are never observed in queenright colonies (for queenright colonies, see MORIMOTO, 1961a, b).

Dominant individuals are said to get more food than subordinates and to have a higher nutritional advantage, which results in ovary development (PARDI, 1948; MORIMOTO, 1960). In the present study, higher-ranked individuals did not enjoy a nutritional advantage, although they laid more eggs than lower-ranked ones. But this does not necessarily mean the absence of nutritional advantage for dominants. It is noteworthy that the offer of flesh by foragers was sometimes rejected by nest mates. This suggests that food supply exceeded the demand and probably nutritional advantage of the dominants did not manifest itself.

Oophagy and the direct interference in ovipositions are two means of egg-laying competitions. WEST-EBERHARD (1969) reported these in foundress associations of *P. fuscatus*, in which the top-ranked and second-ranked foundresses ate eggs laid by subordinates. In my case, an egg-layer often ate one egg before laying her own and there was no case of a female's eating her own egg in all five examples observed.

The gradual increase of egg-layers with colony development is not a phenomenon peculiar to orphan colonies. Laying workers in queenright colonies also gradually increase in this species (MIYANO, unpublished.).

Worker ovipositions occur in two different ecological situations, that is, in normal and in orphan colonies. Recently two other cases of worker ovipositions were reported for this species. First, a worker which ran away from the natal nest occupied an abandoned

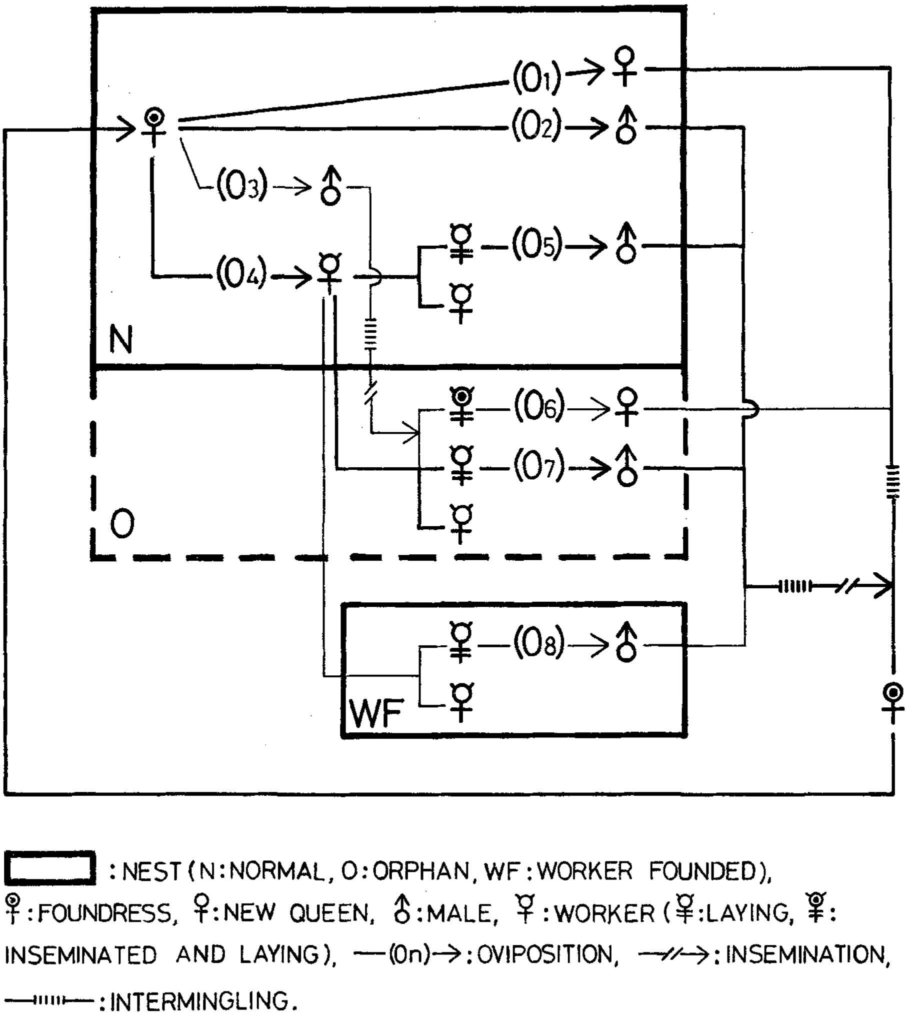


Fig. 6. Schematic representation of the production pathways of workers, new queens, and males in *P.c. antennalis*.

nest and reared her own sons (KASUYA, 1981). Second, worker(s) in an orphan colony copulated with an early emerging male and produced some new queens (KASUYA, 1983). The known reproductive pathways in *P. c. antennalis* are shown schematically in Fig. 6. Three types of colonies are recognized: normal (**N** in Fig. 6), orphan (**O**), and worker-founded (**WF**). Within these we find eight types of ovipositions (O_1–O_8 in Fig. 6). Worker-producing eggs are always laid by the founding queen (O_4; MIYANO, 1983). New-queen-producing eggs are laid by the founding queen (O_1; MIYANO, 1983) and by inseminated workers in orphan colonies (O_6; KASUYA, 1983). It is conceivable that a worker could similarly be inseminated by early emerging males and lay fertilized eggs of new queens in normal and worker-founded colonies, but there has so far been no evidence of such new queen production, although early emergence of males (O_3) was often seen in this species (SUZUKI, 1981b and MIYANO, pers. obs.). Early males were reported in *P. exclamans* by STRASSMANN (1981a). Males develop from five types of eggs (O_2; MIYANO, 1983, O_3; SUZUKI, 1981b, KASUYA, 1983 and MIYANO, pers. obs., O_5; MIYANO, 1983, O_7; present study, and O_8; KASUYA, 1981). The previous (MIYANO, 1983) and the present studies clarified that male production by workers in normal (O_5) and orphan (O_7) colonies were quantitatively very important. Worker oviposition is pointed out to be one of the most important factors affecting social evolution (HAMILTON, 1972; SAKAGAMI, 1975; TRIVERS and HARE, 1976). METCALF (1980) suggested that males produced in orphan colonies may lead normal colonies to produce a female-biased sex ratio of reproductives in *P. metricus*. However, it is necessary to accumulate mor examples of productivities and relative abundances of normal, orphan, and worker-founded colonies for evaluating relative importance of worker oviposition and considering sex ratio in each colony of *P. c. antennalis*.

SUMMARY

Orphan colonies of a Japanese paper wasp, *Polistes chinensis antennalis* PÉREZ, were observed under natural conditions. The results obtained are as follows:

(1) Of 81 colonies active in early August, 25% were orphans.

(2) Two colonies were precisely observed. They were successfully carried on by workers after the queen's disappearance. They developed smaller nests (about 180 cells) and produced no new queens, but produced as many males (about 60) as normal colonies. The number of workers were 35 and 38, respectively.

(3) A linear hierarchy was established among workers through violent dominance-suborination interactions. The dominance order corresponded to the order of emergence.

(4) Dominant workers laid eggs and rarely left the nest. There were serious egg-laying competitions among them by means of egg eating and physical interference.

(5) There was no biased flow of nutrition to dominant individuals, probably due to ample food supply.

(6) Dominance interactions decreased and egg-layers increased in the later period.

(7) Adult workers emerging earlier survived longer than those emerging later.

(8) The brood survivorship curve of the reproductive caste was similar to that in one normal colony where workers actively laid eggs. The curve was characterized by a high egg mortality rate which was caused by active oviposition and egg-eating by multiple egg-layers.

(9) Workers reared nearly all the brood left by the queen. All the adults emerging from this brood were workers.

(10) Reproductive pathways in *P. c. antennalis* were reviewed and emphasis was laid upon the significance of male production by workers both in normal and in orphan colonies.

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女王を失ったフタモンアシナガバチの巣における巣の発展と働き蜂の行動および雄の生産

宮野伸也

女王を失ったフタモンアシナガバチの巣を野外の自然状態で観察し，以下の結果を得た．

(1) 8月初旬における生存巣の約25%は女王を失っていた．

(2) 2つの巣を詳しく観察したところ，巣は女王の消失後も働き蜂によって維持され，順調な発展を続けた．これらの巣では，育室数（約180）は女王のいる正常な巣よりも少なく，新女王は生産されなかったが，雄は正常な巣に匹敵する数（約60匹）が生産された．働き蜂の数は，それぞれ35匹と38匹であった．

(3) 働き蜂の間には，激しい優劣行動による直線的な順位が形成された．この順位は羽化の順と一致した．

(4) 優位個体は産卵を行い，また，ほとんど巣を離れることがなかった．産卵個体の間には産卵をめぐり，食卵と産卵妨害による激しい争いがあった．

(5) 優位個体が食物を優先的に得るようなことはなかったが，これはおそらく食物供給が豊富であったためと思われる．

(6) 働き蜂間の優劣行動は次第に減少し，他方，産卵個体数は次第に増加した．

(7) 初期に羽化した働き蜂は，その後で羽化したものに比べ，はるかに長生きした．

(8) 生殖カストの未成熟期の生存曲線は，働き蜂による活発な産卵のあった正常巣でのそれとよく似ていた。これらの生存曲線は，卵期の高い死亡率によって特徴づけられるが，これは複数の個体による活発な産卵と食卵とによるものである．

(9) 働き蜂は，女王が消失前に産んだ卵および幼虫をほとんどすべて育てた．これらの卵および幼虫から羽化した蜂は，すべてが働き蜂であった．

(10) フタモンアシナガバチにおける子供の生産法を概観し，正常巣および女王を失った巣で行なわれる働き蜂による雄生産の重要性を指摘した．