

## Worker Reproduction and Related Behavior in Orphan Colonies of a Japanese Paper Wasp, *Polistes jadwigae* (Hymenoptera, Vespidae)

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**Abstract** — Worker reproduction and related behavior in 2 orphan colonies of *Polistes jadwigae*, one of which had been maintained by a queen and 5 artificially introduced alien workers, were observed. After the queen loss, a dominance hierarchy was established among workers, and several workers laid eggs without physical interference from other workers. Only males emerged from worker-laid eggs, however, a few new queens were produced from queen-laid eggs. Investment sex ratio of queenright (= normal) colonies (0.27) fell between the 2 theoretical values, corresponding to worker control (0.20 or 0.18) and queen control (0.48 or 0.46) of the sex ratio, both being calculated by considering the excess of males produced in the orphan colonies.

Workers of the social Hymenoptera are specialized for non-reproductive duties, and in higher eusocial species the workers are morphologically modified to perform specific duties (Wheeler 1923). Nevertheless, workers still have ovaries in most of these species. Fletcher & Ross (1985), Bourke (1988) and Choe (1988) reviewed worker reproduction in the social Hymenoptera, and stressed its significance in social evolution.

Worker reproduction may take place under 2 different social situations, that is, in orphan colonies and in queenright colonies (Miyano 1986). Orphan colonies are those which have lost the queen and are maintained by workers (Rau 1929). They are distinguished from colonies in which relief of queens takes place (short term monogyny = serial polygyny), and the succeeding queens are inseminated and lay female eggs (West-Eberhard 1978; Litte 1979; Hughes et al. 1987). Egg layers in orphan colonies, as a rule, lay only unfertilized male eggs, with a few exceptional cases in which fertilized eggs had been produced (Kasuya 1983; Suzuki 1985). The relief of queens occurs mainly in tropical and subtropical social species (West-Eberhard 1969; Jeanne 1972; Strassmann 1981; Turillazzi et al.

1985; Yamane 1986; Hughes et al. 1987; Gadagkar 1990), whereas orphan colonies are almost always restricted to temperate social species (Free 1955; Landolt et al. 1977; Turillazzi 1980; Sugiura et al. 1983; Suzuki 1985; Ross 1985; Miyano 1986).

During a 4-year study, I observed 2 orphan colonies of a Japanese paper wasp, *Polistes jadwigae*. In the present paper, I show behavioral and ecological data of these orphan colonies and discuss the significance of male production in orphan colonies in relation to the social evolution of wasps.

### Materials and Methods

Observations were carried out in rural areas in Oyama, Seki City, Gifu Pref., Japan. *P. jadwigae* nested on small trees and buildings. Although pleometrosis is sometimes reported for this species (Yoshikawa 1957; Kasuya 1981), over-wintered queens always start their nests haplometrotically (by single foundress) in this area.

Two colonies, No.7970 and No.8022, both of which lost their queens late in June, were, as a

rule, observed every day by recording nest maps from 5 June to 30 August 1979, and from 22 May to 11 August 1980, respectively. In No.7970, 5 teneral workers, which emerged in other colonies, were artificially introduced to prevent a colony failure due to heavy loss of first cocoons before the queen loss. Oviposition, hatching, cocoon spinning, emergence, death of individuals, and other events were regarded as having occurred on the days when they were recorded on nest maps. For No.7970, all wasps were marked individually with color dots without anesthesia, and their intranidal behavior was observed 5 times (18 June, 4 h; 23 June, 4 h; 10 July, 2 h; 3 August, 4 h; 25 August, 2.25 h). Dominance interactions, time of leaving from and returning to the nest, loads brought back by foragers, food exchange between individuals, and oviposition were recorded, except on 3 and 25 August, when there were so many wasps that dominance interactions and food exchange could not be checked. All nest members from No.8022 were collected on 11 August, and females were dissected to assess their ovarian development.

## Results

### 1. Developmental Processes of Colonies

In No.7970, the first 5 cocoons died one after another from unknown causes and no workers emerged. The mortality factor was probably parasitism by dipteran (*Euvespivora* sp.) larvae, because they were confirmed to infest 3 out of 7, and 9 out of 12 cocoons of the first brood in 2 other colonies, respectively. One teneral worker (emerged on 12 June from No.7946) was artificially introduced into the colony on 13 June. She was accepted by the queen without antagonism. Another 4 teneral workers (1 emerged from No.7968 and 3 from No.7946) were introduced between 14 and 18 June. They were also accepted by the queen and the worker(s). The introduced workers worked for the colony and contributed to nest growth.

Queens of both nests, No.7970 and No.8022, disappeared from the nests on 23 June 1979 and 25 June 1980, respectively, when there were 5

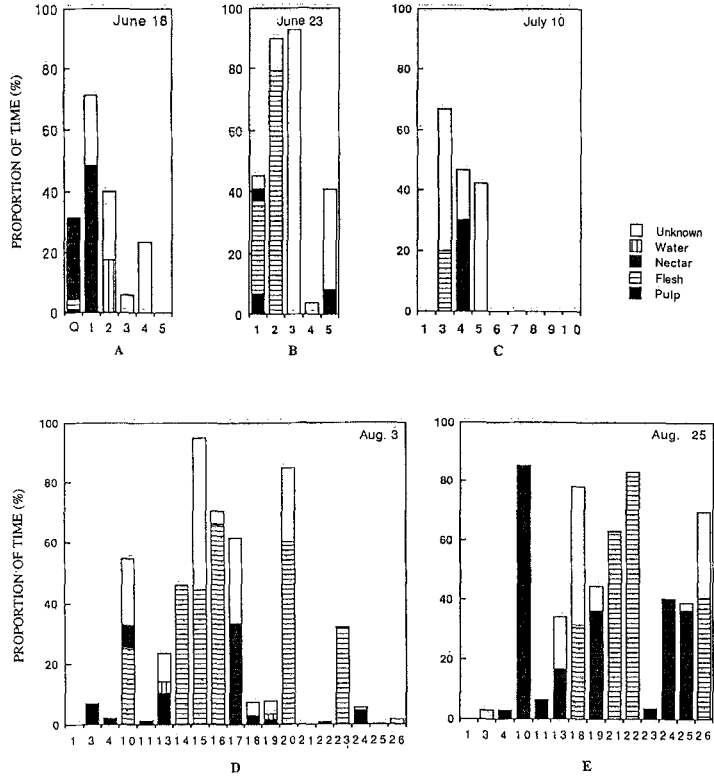
workers in each colony. Two workers of No.7970 had already begun foraging by the day of the queen loss (Fig. 1 A). Although no behavioral observation was made on No.8022, 2 older workers were considered to be working because workers usually begin foraging 2 to 3 days after their emergence (Miyano, unpublished). Judging from the colony size and colony composition at the time of the queen loss (Table 1), both colonies had developed normally by this time, except for the high mortality of cocoons in No.7970.

After the disappearance of the queen, eggs were laid and immatures were reared by workers, and the colonies grew. The 2 nests finally attained 167 cells (No.7970) and 151 cells (No.8022) (Fig. 2).

These 2 nests, among 11 observed colonies, were the only colonies that were orphaned in the period of 4 years ( $2 / 11 = 18.2\%$ ).

### 2. Behavior of Workers in No.7970

The frequency of dominance-subordination interactions among workers rose markedly shortly after the disappearance of the queen. The dominant individual antennated, licked, and sometimes bit the body of the opponent, which assumed a motionless posture and pulled in its antennae and legs. The frequency increased from 3 acts / h on 18 June (5 days before the queen's disappearance) to 24 / h on 23 June (the day of disappearance) (Tables 2 and 3). The actual increase of dominance interactions was more abrupt, because most of them (89 out of 98) occurred over a period of 2 h about 1.4 h after the disappearance of the queen on 23 June (44.5 / h). On 10 July there were still many interactions (21 / h, Table 4). The older workers usually dominated the younger ones, except in one case. The relationship among all individuals, however, was not clear because dominance-subordination interactions did not occur in every pair of individuals. The exception was that the rank of W4 was considered to be higher than W2 on 23 June (Table 3). This reversal was suggested by the fact that although W2 dominated W4 once, W4 dominated W1 (top dominant) once and laid 2 eggs. Most dominant acts after the disappearance of



**Fig. 1** Comparison of extranidal activities of individual wasps in No. 7970. Proportion of time spent in extranidal activities to observation time is shown. A: based on a 4 h observation on 18 June (5 days before the queen loss), B: 4 h, 23 June (the day of the queen loss), C: 2 h, 10 July (17 days after the queen loss), D: 4 h, 3 August (41 days after), and E: 2.25 h, 25 August (63 days after). Q: queen; 1-26: daughters.

**Table 1** Compositions of 2 orphan colonies on the day of the queen loss and of 4 normal colonies at similar dates.

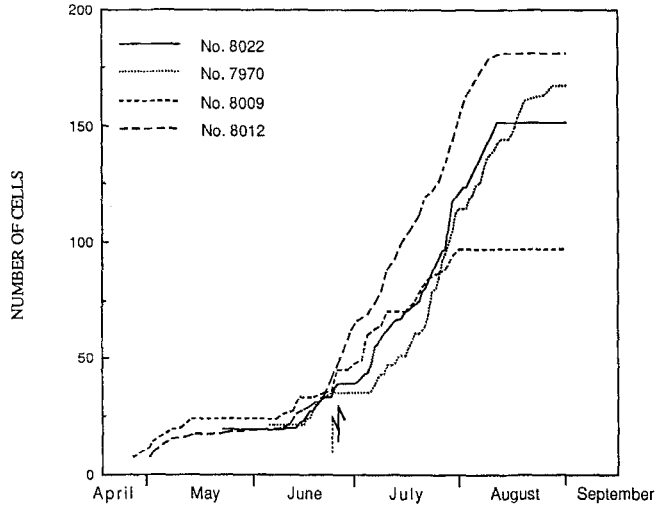
	Orphan colony		Normal colony*4			
	No. 7970*3	No. 8022	No. 7974	No. 8009	No. 8012	No. 8227
Date	June 23	June 25	June 24	June 24	June 24	June 24
No. cells*1	35	39	28 + 2	41 + 1	43 + 1	54
No. eggs*2	8 + 5	12 + 1	8 + 2	13 + 3	16 + 1	20 + 5
No. larvae*2	15	19 + 4	15 + 2	20 + 3	21 + 4	28 + 1
No. cocoons	6	5	4	7	5	6
No. empty cells	6	3	1	1	1	0
No. workers	5	5	4	5	7	9
Age of the oldest worker (days)	10	8	4	8	10	12-13

\*1: No. cells with only bases built are designated by + n.

\*2: Nos. eggs and larvae which were present on cocoon caps are designated by + n.

\*3: Five foreign workers were introduced.

\*4: Miyano, unpublished.



**Fig. 2** Changes in the number of cells in 2 orphan (Nos. 7970 and 8022) and 2 normal (Nos. 8009 and 8012, Miyano, unpublished) colonies. Arrows indicate the days of the disappearance of queens.

**Table 2** Number of dominance interactions among the queen and workers, and number of ovipositions in No.7970. Based on 4 h of observation on 18 June (5 days before the queen loss).

Dominant individual	Age (days)	Subordinate individual						Total dominations	Ovipositions
		Q	1	2	4	3	5		
Q	—	—	0	0	0	0	0	0	0
1	6	0	—	1	2	0	0	3	0
2	5	0	0	—	0	0	2	2	0
4	2-3	0	0	0	—	0	2	2	0
3	2-3	0	0	0	0	—	5	5	0
5	1	0	0	0	0	0	—	0	0
Total submissions		0	0	1	2	0	9	12	Total 0

**Table 3** Number of dominance interactions among workers and number of ovipositions in No.7970. Based on 4 h of observation on 23 June, during which the queen disappeared from the nest.

Dominant worker	Age (days)	Subordinate worker					Total dominations	Ovipositions
		1	4	2	3	5		
1	11	—	74	3	0	3	80	0
4	7-8	1	—	0	5	10	16	2
2	10	0	1	—	0	0	1	0
3	7-8	0	0	0	—	1	1	0
5	6	0	0	0	0	—	0	0
Total submissions		1	75	3	5	14	98	Total 2

Table 4 Number of dominance interactions among workers and number of ovipositions in No. 7970. Based on 2 h of observation on 10 July (17 days after the queen loss).

Dominant worker	Age (days)	Subordinate worker										Total dominations	Ovipositions
		1	4	3	5	6	7	8	9	10			
1	28	—	20	2	0	7	5	1	2	2	39	1	
4	24-25	0	—	1	1	0	1	0	0	0	3	1	
3	24-25	0	0	—	0	0	0	0	0	0	0	0	
5	23	0	0	0	—	0	0	0	0	0	0	0	
6	6	0	0	0	0	—	0	0	0	0	0	0	
7	5	0	0	0	0	0	—	0	0	0	0	0	
8	4	0	0	0	0	0	0	—	0	0	0	0	
9	3	0	0	0	0	0	0	0	—	0	0	0	
10	2	0	0	0	0	0	0	0	0	—	0	0	
Total submissions		0	20	3	1	7	6	1	2	2	42	Total 2	

Table 5 Direction of flow of flesh and nectar between workers of known dominance rank in No.7970.

	23 Jun.	10 Jul.	3 Aug.	25 Aug.	Total
Observation time (h)	4	2	4	2.25	12.25
Transfer of flesh					
lower to higher	3	0	6	5	14*
higher to lower	4	1	11	3	19*
Transfer of nectar					
lower to higher	2	13	3	1	19**
higher to lower	1	3	1	1	6**

\*: Difference is not significant ( $\chi^2 = 0.758$ ,  $P > 0.1$ ).

\*\* : Difference is significant ( $\chi^2 = 6.635$ ,  $P < 0.01$ ).

the queen were performed by the top-ranked worker (119 / 140 = 0.85), and 79 % (94 / 119) of acts were directed toward the second-ranked worker.

Foraging activity of the top-ranked worker (W1) changed markedly after the disappearance of the queen (Fig. 1). W1 frequently left the nest and came back with nectar, nesting material and/or flesh before the queen loss (18 and 23 June), but she never left the nest on 10 July, 3 August, and 25 August. Another 2 higher-ranked individuals (W3 and W4) became less active in foraging. Extranidal activities were equally performed by lower-ranked individuals.

Oviposition by workers was observed 2 times (0.5 eggs / h, Table 3) on the day of the disappearance of the queen, 2 (1.0 / h, Table 4)

on the 17th day, and 5 (1.25 / h) on the 41st day. No eggs had been laid during a 2.5-h observation on the 63rd day. In total, 13 ovipositions were observed among 4 individuals (W1:5, W4:6, W3:1, W11:1). Most eggs were laid by the top and the second dominants. There was no physical interference directed against the egg layers, even if they were lower-ranked individuals. Oophagy was observed 3 times (once performed by W1, and twice by W4), but the identities of the eaten eggs' mothers were unknown. It was evident from the record of cell maps that many eggs were eaten.

Some nutritional advantage of higher-ranked individuals was recognized (Table 5). Flow of nectar from lower-ranked to higher-ranked individuals predominated. Flow of flesh was not

biased in either direction.

Twenty-one females emerged in colony No.7970. Except for the first 3, all foraged for nesting material and/or flesh. Although the first 3 did not forage during a short (2 h) observation on 10 July, they were also regarded as workers, since, in this species, new queens usually emerge after a series of worker emergences (Miyano, unpublished). Consequently, all 21 females emerged in No.7970 after the queen loss were considered to be workers.

### 3. Survival of Immatures Produced and Left by the Queen

The fate of eggs laid and left by the queen was different between the 2 colonies. In No.7970, which was maintained by 5 artificially introduced alien workers, all 13 of the queen-laid eggs were completely destroyed by workers within a few days after the queen loss, while in No.8022 no such mass destruction of queen-laid eggs took place, and 12 out of 13 eggs grew to adults. Larvae and cocoons left by the queen were not destroyed in either colony. Twenty-one and 34 females emerged in No.7970 and No.8022, respectively, from the brood left by the queen. They were all workers in No. 7970 as already mentioned, whereas in No.8022, they included 24 workers and 10 new queens (see below).

### 4. The Number of Reproductives Produced

Table 6 presents the number of each caste and sex produced in the 2 orphan colonies as compared with those of the 4 normal (= queenright) colonies (data from Miyano, unpublished). In No.7970, the distinction between the castes was based on behavioral observations, as already mentioned. In No.8022, the distinction was arrived at by dissection of the wasps collected on 11 August. Forty-eight adults were estimated to have emerged from No.8022 before collection. Thirty of these (21 females and 9 males) were captured, and all females were dissected. Two had developed ovaries with 10 and 9 mature eggs, respectively, and were regarded as false queens (Table 7). Nine had thread-like ovaries, 3 of which had somewhat worn wings, and were regarded as workers. The other 10 had thread-like ovaries and thick fat bodies with fresh wings, and were considered to be new queens. Eighteen wasps, which were not captured because of their absence on 11 August, were regarded as workers that had died, because the reproductives usually remained on the nest until later in the season.

The number of males produced was estimated as follows: When destroyed by man on 30 August, No.7970 had 71 adult males, 52 cocoons, 51 larvae, and 33 eggs. As 30 August was near the end of the nesting season, only cocoons were assumed to be likely to survive if the nest had not been destroyed. These cocoons would be males, because this nest produced only

Table 6 Numbers of adults produced, numerical sex ratio (males / (mles + new queens)) and cells constructed in 2 orphan and 4 normal colonies of *P. jadvigae*.

Colony	No.7970	No.8022	No.7974 <sup>#</sup>	No.8009 <sup>#</sup>	No.8012 <sup>#</sup>	No.8227 <sup>#</sup>
Condition	orphan	orphan	normal	normal	normal	normal
a) No. workers	26*	29	16	19	24	35
b) No. new queens	0	10	35	63	73	32
(b/a)	0.00	0.34	2.19	3.32	3.04	0.91
c) No. males	123	70	11	17	45	29
(c/a)	4.73	2.41	0.69	0.89	1.88	0.83
d) Numerical sex ratio	1.00	0.88	0.24	0.21	0.38	0.48
d) No. of cells	167	151	75	97	181	174
(d/a)	6.42	5.21	4.69	5.11	7.54	4.97

\*: Five workers introduced artificially are included.

#: Miyano, unpublished.

Table 7 Result of dissection of 21 females of No.8022 collected on 11 August.

Individual No.	On nest (N)/ Returning (R)* <sup>1</sup>	Degree of ovariole development** <sup>2</sup>	Length of ovarioles (mm)	Deposition of fat body	Wing wear* <sup>3</sup>
1	R	U	15		0
2	R	U	9		0
3	R	U	11		0
4	R	U	15		0
5	N	U	12		II
6	N	U	12		0
7	N	U	12	+	0
8	N	U	15	+	0
9	N	D(10)	25		0
10	N	U	15	+	0
11	N	U	17		0
12	N	U	12		I
13	N	U	15	+	0
14	N	U	12	+	0
15	N	U	16	+	0
16	N	U	10		II
17	N	U	14	+	0
18	N	U	12	+	0
19	N	U	15	+	I
20	N	D(9)	25		II
21	N	U	15	+	0

\*<sup>1</sup>: The wasp was caught on the nest (N) or in air at time of returning to the nest (R).

The latter case indicates the strong probability that she was a worker.

\*<sup>2</sup>: U = Undevelopped, D = developped, ( ) = number of matured eggs.

\*<sup>3</sup>: O = no wear, I = slight wear, II = moderate wear, III = heavy wear, IV = extremely heavy wear.

males after 6 August. So the number of males produced in No.7970 was estimated at 123. No.8022 had 9 adult males and 143 immatures, i.e., 40 cocoons, 65 larvae, and 38 eggs at the nest collection. Using an average emergence rate of a brood (= the number of adults grown from a brood/the number of that brood) in that season in 4 normal colonies, (0.426; Miyano, unpublished), the expected number of emergences was estimated at 61 (= 143 × 0.426). They were considered to be males, because 38 of 40 cocoons and 34 of 36 fifth instar larvae were males (sexed by a method described by Yamane 1976), while the sex of 2 cocoons and 2 larvae could not be determined. Thus, the total number of males to be produced in No.8022 was estimated at 70.

Although a small number of new queens were produced in No.8022, males were the principal reproductive output in orphan colonies (Table 6). The number of males produced was nearly the same as the total number of new

queens and males produced per normal colony (Table 6). Worker efficiency (number of reproductives per worker) was also similar between orphans and normals ( $\bar{x} = 3.74$  vs.  $\bar{x} = 3.44$ ).

## Discussion

The results show that behavior and reproduction of workers in orphan colonies of *P. jadwigae* were basically similar to those in orphan colonies of *P. chinensis antennalis* documented by Miyano (1986). There were, however, some differences between them.

(1) In both species a dominance hierarchy was established among nest mates, and more than 1 worker laid eggs, but there was no physical interference among *P. jadwigae* workers, as was frequently seen among the egg layers in *P. chinensis antennalis*. Behavior observations were made only for one colony into which 5 alien workers were introduced. However, I con-

sider that this does not affect the basic features, because coexistence of unrelated individuals in a colony may increase the hostility among nest mates, rather than decrease it, and the coexistence of more than 1 egg layer was confirmed by dissection in the other *P. jadvigae* orphan colony, which contained no alien workers.

(2) In contrast to orphan colonies of *P. chinensis antennalis* that produced males alone (Miyano 1986), an orphan colony of *P. jadvigae* produced a small number of new queens in addition to males. This difference may be a result of the differing reproductive ecologies of the 2 species. In *P. chinensis antennalis*, eggs which became reproductives were laid about 20 days after the first emergence of workers. This means that there were no reproductive eggs (eggs destined to develop into new queens or males) in the colony when it was orphaned (Miyano 1983). In *P. jadvigae*, however, the queen began to lay reproductive eggs about 7 days before the first worker emergence (Miyano, unpublished). Therefore, some reproductive eggs may have already existed at the time of orphaning.

(3) The final colony size and colony productivity of orphan colonies of *P. jadvigae* did not differ from those of normal colonies when they were reduced to about 1/3 of normals in *P. chinensis antennalis* (Miyano 1986). This difference is also explained by the different timing of deposition of reproductive eggs. Because deposition of worker eggs ceased before the worker emergence (Miyano, unpublished), and the brood had not been destroyed by workers after the queen loss, orphaning in *P. jadvigae* did not reduce the number of workers produced. In *P. chinensis antennalis*, however, the queen loss before the deposition of worker eggs had been completed resulted in a reduction of worker production in orphan colonies (Miyano 1986). As reproductive productivity may be positively correlated with the size of the worker force, and if worker efficiency (number of reproductives/worker) does not differ between normal and orphan colonies, it is understandable that the number of reproductives raised in orphan *P. jadvigae* colonies was not different from that in normal colonies.

(4) Worker efficiency of orphan colonies in rais-

ing reproductives did not decrease in *P. jadvigae*, but declined to about 2/3 of that in normal colonies in *P. chinensis antennalis* (Miyano 1986). A severer competition for oviposition among workers in orphan colonies, as exemplified by physical interference, probably reduced worker efficiency in *P. chinensis antennalis*.

Eggs left by the queen were completely destroyed by workers in an orphan colony (No.7970) of *P. jadvigae*. In this colony, the first 5 workers, which dominated the colony after the queen loss, were aliens which had been artificially introduced into the colony. Some new queens would have been produced if no oophagy had taken place. The workers should opt not to raise unrelated reproductive individuals. Queens of *Polistes fuscatus* selectively destroyed the brood which would have become reproductives when they switched to, or usurped, nests of unrelated queens (Klahn & Gamboa 1983; Klahn 1988).

It is advantageous for workers to produce their own sons when they cannot raise sisters (which are more related to them than their sons). This advantage of male production in orphan colonies may select for the retention of worker ovaries in the genus *Polistes*.

It is inferred, however, that there was a severe conflict among workers who laid eggs. Laying workers leave sons with a relatedness of 1/2, while non-laying workers raise males with a maximum relatedness of 3/8 to them (if a monogynous queen mates multiple males, relatedness decreases to a minimum of 1/8). Aggressive interactions among workers after the queen loss confirm this inference. Hostile interactions among workers have also been observed in orphan colonies of other social Hymenoptera (Free 1955; Landolt et al. 1977; Matsuura 1984; Miyano 1986).

According to kin selection theory (Hamilton 1964), investment sex ratio in the social Hymenoptera should be biased at 1:3 (male: female) when all nests are monogynous, females mate only once, and workers can determine the colony sex ratio (Trivers & Hare 1976; Iwasa 1981). However, when orphan colonies produce only, or mostly, males, and the proportion of orphan colonies is high, the investment sex ratio of queenright (= normal) colonies



changes to produce more females with supplementing excess males in the population. Iwasa (1981) examined the role of sex ratio in the evolution of eusociality in the Hymenoptera by using a game-theoretical model. The reasoning of his model is applicable to an examination of the effect of male production in orphan colonies on the sex ratio in queenright colonies. If the sex ratio of queenright colonies is determined by workers, it becomes

$$Sr = \frac{1}{4} + \frac{1}{4} \left\{ \frac{CQ_o (1-Fr)}{(CQ_q + Mq) Fr} \right\} - \frac{3}{2 \times 4} \left\{ \frac{M_o (1-Fr)}{(CQ_q + Mq) Fr} \right\} \dots\dots\dots (1)$$

where, Sr, Qq, Mq, Qo, Mo, C and Fr represent investment sex ratio (ratio of males), number of new queens produced in a queenright colony, number of males produced in a queenright colony, number of new queens produced in an orphan colony, number of males produced in an orphan colony, the relative cost of a new queen to a male, and the frequency of queenright colonies in the population, respectively. Equation (1) corresponds to equation (19) in Iwasa (1981). If the sex ratio of queenright colonies is determined by the queen, it becomes

$$Sr = \frac{1}{2} + \frac{1}{2} \left\{ \frac{CQ_o (1-Fr)}{(CQ_q + Mq) Fr} \right\} - \frac{1}{2 \times 2} \left\{ \frac{M_o (1-Fr)}{(CQ_q + Mq) Fr} \right\} \dots\dots\dots (2)$$

which corresponds to (22) at  $t=1$  in Iwasa (1981). Replacing  $Q_o$  by 0 and  $\left\{ \frac{M_o (1-Fr)}{(CQ_q + Mq) Fr} \right\}$  by  $\beta$ , we obtain  $Sr = 1/2 - \beta/4$ , which is just the same as the sex ratio equation presented by Taylor (1981). For the derivation of equations (1) and (2), see Appendix.

The above theoretical predictions are tentatively examined by using the present results, even though the data are limited to a very small number of colonies. Table 8 presents relevant data for *P. jadvigae*. The value of C, 1.37, was determined by dividing the average dry weight of the females by that of the males (Miyano, unpublished). The females and males used for the calculation were collected on a nest in late summer, therefore they had spent some length of time on the nest after emergence. Suzuki (1986) estimated C for this species as 0.981 by using average live weights at emergence. Because reproductives would get some amount of nutrient from workers and accumulate it in the body during their stay in the nest, the present estimate ( $C = 1.37$ ) may be better. Theoretically, Sr has a value of 0.20 if workers control the sex ratio, and 0.48 if the queen controls it, provided only productivity from No.8022 is used in the calculation. When average productivity of 2 colonies is used, the corresponding values of Sr become 0.18 and 0.46, respectively. In any case, the observed value of  $Sr = Mq / (CQ_q + Mq) = 0.27$  lies between the two theoretical

Table 8 Average numbers of reproductives in 4 normal and in 2 orphan colonies, frequency of each type of colony, and the relative cost of a female to a male in *P. jadvigae*.

	Normal colony	Orphan colony
No. new queens	50.75	10
No. males	25.5	70*, 89.65**
Frequency of colonies	0.818	0.182
Relative cost	1.37	1.37

\*: Value of No.8022 only

\*\* : Average of 2 colonies. The number of males in No.7970 was reduced to  $123 - 10 \times 1.37 = 109.3$  because some new queens and a smaller number of males would have been produced in this colony if alien workers had not destroyed the queen-laid eggs. I assumed the same number of new queens (10) in No.7970 as in No.8022.

values. This result is interesting, but we cannot say anything more on the worker control of sex ratio until more data had been accumulated.

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## Appendix

### Sex Ratio in Queenright Colonies

According to Iwasa (1981), inclusive fitness of a worker ( $\emptyset_w$ ) and the queen ( $\emptyset_q$ ) in a queenright colony is expressed as follows by introducing the relative cost (C) of a new queen to a male, when workers do not lay eggs in that colony:

$$\begin{aligned}\emptyset_w &= \lambda_o + \frac{1}{4}BSrRm + \frac{3}{4}\frac{B(1-Sr)}{C}Rf \\ &= \lambda_o + \frac{1}{4}BSr(Rm - \frac{3Rf}{C}) + \frac{3BRf}{4C}, \quad (A1)\end{aligned}$$

$$\begin{aligned}\emptyset_q &= \frac{1}{2}(Mq + CQq)SrRm \\ &+ \frac{1}{2}\frac{(Mq + CQq)(1-Sr)}{C}Rf \\ &= \frac{1}{2}(Mq + CQq)Sr(Rm - \frac{Rf}{C}) \\ &+ \frac{1}{2C}(Mq + CQq)Rf, \quad (A2)\end{aligned}$$

where  $\lambda_o$ , B, Rm, and Rf are the base-line, the reproductive output of the queen increased by labor of a worker, the reproductive success of a male, and the reproductive success of a new queen (the other symbols are the same as in the text). The ratio of the reproductive success of a male to that of a new queen in a population is

$$\begin{aligned}\frac{Rm}{Rf} &= \frac{\frac{(Mq + CQq)(1-Sr)Fr}{C} + Qo(1-Fr)}{(Mq + CQq)SrFr + \frac{1}{2}Mo(1-Fr)} \\ &= \frac{1}{C}\frac{(Mq + CQq)(1-Sr)Fr + CQo(1-Fr)}{(Mq + CQq)SrFr + \frac{1}{2}(1-Fr)}, \quad (A3)\end{aligned}$$

when orphan colonies produce males from worker-laid eggs and new queens from queen-laid eggs and when the frequency of these colonies is  $(1 - Fr)$ .

If sex ratio of queenright colonies is determined by workers,  $Sr$  in equation (A1) is  $0 < Sr < 1$ , if and only if

$$Rm - \frac{3Rf}{C} = 0. \quad (A4)$$

Solving equations (A3) and (A4) for  $Sr$ , we get

$$Sr = \frac{1}{4} + \frac{1}{4} \left\{ \frac{CQo(1-Fr)}{(CQq+Mq)Fr} \right\} - \frac{3}{2 \times 4} \left\{ \frac{Mo(1-Fr)}{(CQq+Mq)Fr} \right\} \quad (A5)$$

If sex ratio of queenright colonies is determined

by the queen,  $Sr$  in equation (A2) is  $0 < SR < 1$ , if and only if

$$Rm - \frac{Rf}{C} = 0. \quad (A6)$$

Solving the equations (A3) and (A6) for  $Sr$ , we get

$$Sr = \frac{1}{2} + \frac{1}{2} \left\{ \frac{CQo(1-Fr)}{(CQq+Mq)Fr} \right\} - \frac{1}{2 \times 2} \left\{ \frac{Mo(1-Fr)}{(CQq+Mq)Fr} \right\}. \quad (A7)$$

The second term of the right side of equations (A5) and (A7) expresses the effect of the new queens produced in orphan colonies. Similarly, the third term does that of the males.

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