

COMPARISON OF LIFE TABLES BETWEEN THE SOLITARY
EUMENID WASP *ANTERHYNCHIUM FLAVOMARGINATUM*
AND THE SUBSOCIAL EUMENID WASP *ORANCISTROCERUS*
DREWSENI TO EVALUATE THE ADAPTIVE SIGNIFICANCE
OF MATERNAL CARE¹

Takao ITINO

Laboratory of Applied Entomology, Faculty of Agriculture
Kagawa University, Miki-tyo, Kita-gun
Kagawa 761-07, Japan

INTRODUCTION

Three possible routes to eusociality in Hymenoptera have been proposed. One is the subsocial route, which involves a continuum of nesting habits from progressive provisioning (subsocial form), through brief encounters between mother and daughters, to continuous cooperative associations of mother and daughters (WHEELER, 1923; BROCKMANN, 1984). The second route is essentially the same except that the encounters between mother and daughters occur not through subsocial form but directly from mass provisioning (solitary form) (LIN and MICHENER, 1972). The third is the semisocial route, which involves increasing levels of association among females of the same generation (MICHENER, 1974). In all hypotheses, selective pressures from predators and parasitoids are thought to be a major promoter of social evolution (EVANS, 1977). The adaptiveness of cooperative nesting of female wasps and bees has recently been studied quantitatively (GAMBOA, 1978; LITTE, 1981; LIN, 1964; SAKAGAMI, 1977). Although SAKAGAMI and MAETA (1977) showed the adaptive significance of anti-parasitoid maternal behavior in two subsocial *Ceratina* bees, there was no comparable study for subsocial wasps. Itô (1980) compared survivorship curves of several Hymenoptera species and suggested hypothetically that the more advanced the parental care, the lower the brood mortality at early stages. But he did not show how the parental care decreased the early mortality rate.

The present study compares differences in life tables between the solitary eumenid wasp *Anterhynchium flavomarginatum* and the subsocial eumenid wasp *Orancistrocerus drewseni*, to evaluate the adaptive significance of maternal care in the subsocial eumenid wasp. These two closely related eumenid wasps appear to be suitable for such a comparison because they cohabit the same nesting sites but differ in their degree of maternal care. Like in most other hunting wasps, all dead brood (eggs, larvae, prepupae and

¹ Contribution to the ecological studies of the eumenid wasps. I.

pupae) and their enemies generally remain in the nest and, thus, dissection of nests provides detailed information on mortality factors and the developmental stages at which host wasps were attacked. Freeman and his co-workers promoted the life table analysis of solitary wasps by this method (e.g., FREEMAN, 1973, 1977, 1981; FREEMAN and TAFFE, 1974). I specifically investigated whether maternal care by the subsocial eumenid wasp decreases brood mortality as compared with the solitary one.

MATERIALS AND METHODS

General life history

Anterhynchium flavomarginatum SMITH is the solitary eumenid wasp that ranges from southern Hokkaido, Japan to Taiwan (YAMANE, 1981). *Orancistrocerus drewseni* SAUSSURE is the subsocial eumenid wasp found in Honshu, Sikoku and Kyusyu, Japan (YAMANE, 1982). The study area, Kyoto, is in the center of distribution for both eumenids. Both wasps are abundant in the study area. In the subsocial eumenid, no males have been found in Japan (YAMANE, 1982), thereby suggesting parthenogenetic reproduction.

The solitary eumenid makes mud nests in open, slender bamboo internodes and in caterpillar's borings in twigs or branches. The diameter of these hollows is usually 0.8 to 2.0cm. In contrast, the subsocial eumenid constructs mud nests in larger cavities, e.g. bamboo internodes of 0.8–4.0 cm diameter, hollows in tree trunks, or crevices on cliffs.

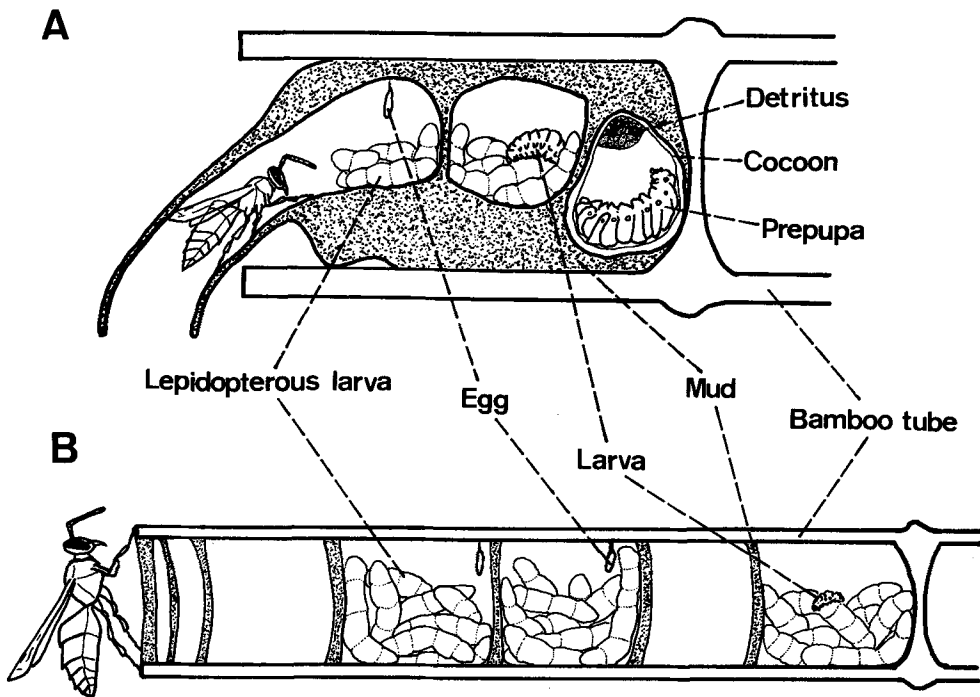


Fig. 1. Nest structures of the subsocial eumenid wasp *O. drewseni* (A) and of the solitary eumenid wasp *A. flavomarginatum* (B).

The nests of both wasps contain cells that are separated linearly by mud walls (Fig. 1).

A female of the solitary eumenid firstly lays an egg in the innermost cell and then provisions the cell containing her egg with paralyzed lepidopterous larvae for one or two days. After sealing the innermost cell with a mud wall, the female starts the second oviposition. In contrast, a female of the subsocial eumenid begins provisioning just before the egg hatches and continues provisioning for about one week until the larva grows to instars 3–5.

The solitary eumenid is univoltine in Kyoto. New adults emerge from June to July. Soon after emergence, females normally mate in front of their nests. Oviposition occurs from mid August to late October. Prepupae diapause in cells. The longevity of females is 2 to 3 months. One female can lay 20 to 30 eggs during her entire reproductive period. The subsocial eumenid, however, is bivoltine. Females of the first generation emerge from mid to late June. Oviposition begins about four days after emergence and continues until mid to late August. Females of the second generation, which emerge in August, oviposit until mid October. The diapause stage is the prepupa. The longevity of first generation females is 2 to 3 months and second generation females, 1 to 1.5 months. The number of eggs laid per female is 6 to 8 in both generations. In both wasps, the developmental periods are as follows; 3–4 days as an egg, 5–9 days as a larva, 20–30 days as a prepupa of the first generation of the subsocial eumenid and 8–9 months as a overwintering prepupa in both wasps, 5–10 days as a pupa.

Study area

Iwakura and Ohara in the northern suburbs of Kyoto were selected as the study area (Fig. 2). In the study area, rice paddies were common along rivers. At the edges of rice paddies, there were several dozen small open sheds in which farmers stored poles. Land ridges in the study area were occupied mainly by temperate deciduous trees, some of which were host plants of lepidopterous larvae hunted by the eumenid wasps. The remaining trees were Japanese cedar and Japanese red pine.

In the study area, females of the subsocial eumenid constructed nests mainly at the cut end of bamboo poles stored in the small sheds (Fig. 1). The inner diameters of bamboo poles were 2.0–5.0 cm. These large bamboo poles were unavailable for the solitary eumenid, which used bamboo internodes smaller than 2.0 cm. The number of available bamboo poles was 40–100 per shed. In addition, I placed a bundle of bamboo internodes ($l=10\text{--}25$ cm and $\phi=0.4\text{--}2.0$ cm), at each of the sheds before the beginning of the wasp breeding season. This nest trap was available for both kinds of wasps. The number of internodes was 50–100 per nest trap.

There were about 150 sheds containing bamboo poles (referred to as “natural nest sites”) in the study area. Of these, 21 sheds were chosen for collection during 1980–1983. In those sheds lacking bamboo poles, there was no nesting substratum available for the two wasp species. I set one nest trap at each of 20 such empty sheds during 1980–1983 (mostly for one year per shed) in order to gather life table data for newly-made nest sites.

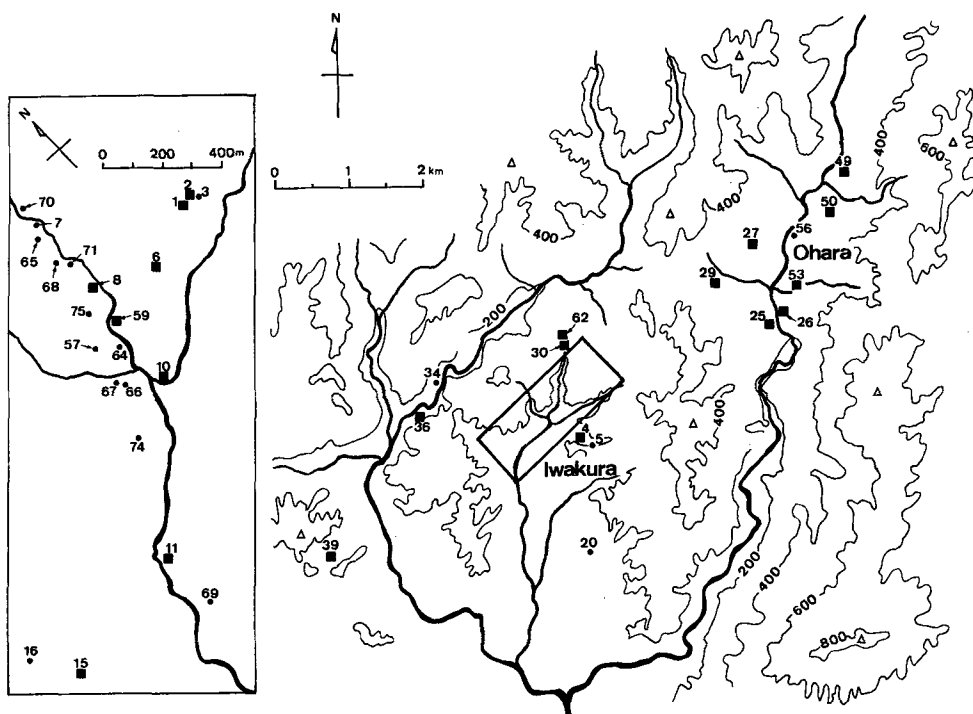


Fig. 2. Map of the study area, the northern part of Kyoto, showing the location of natural nest sites (closed squares) and additional nest sites (closed circles) with the site number. The enlarged map of the Iwakura sub-area is shown in the rectangle. There were three nest sites out of this map.

I refer to these as “additional nest sites”. Consequently, there were two types of nesting sites for the solitary eumenid (nest traps at natural nest sites and at additional nest sites), and three types for the subsocial eumenid (bamboo poles at natural nest sites, nest traps at natural nest sites, and nest traps at additional nest sites).

Collection and Dissection

Nests of the two eumenid wasps were collected during the winters of 1980–1983 (Table 1). I collected all of the nests of the solitary eumenid (Table 1). In total, 114 nests (204 cells) were collected from nest traps at the natural nest sites and 127 nests (318 cells) from nest traps at the additional nest sites. In the subsocial eumenid, collection was done by random sampling at nest sites that contained abundant nests. The average percent of collection was 37% (126 nests out of 337 total nests located). In total, 72 nests (186 cells) were collected from the cut end of bamboo poles in natural nest sites, 28 nests (72 cells) from nest traps at the natural nest sites and 26 nests (69 cells) from nest traps at the additional nest sites. The collected nests were dissected to determine the cause of brood mortality and the developmental stages at which the eumenid wasps had died. As mentioned above, the dead bodies of brood wasps and their enemies remained in the nest. All live wasps, as well as their parasitoids and predators, were

Table 1. Numbers of nests located and nests (cells) dissected of the solitary eumenid *A. flavomarginatum* and the second generation of the subsocial eumenid *O. drewseni* during 1980–1983.

Wasp species	Type of nest site	Nest substratum	1980		1981		1982	
			No. nests located	No. nests (cells) dissected	No. nests located	No. nests (cells) dissected	No. nests located	No. nests (cells) dissected
Solitary eumenid	Natural nest site	nest traps	7	7(15)	40	40(74)	6	6(6)
	Additional nest site	nests traps	9	9(18)	65	65(192)	14	14(46)
Subsocial eumenid	Natural nest site	bamboo poles	79	44(117)	51	3(6)	41	4(7)
	Natural nest site	nest traps			10	10(16)	8	8(29)
	Additional nest site	nest traps			13	8(24)	32	17(42)
Wasp species	Type of nest site	Nest substratum	1983		Total			
			No. nests located	No. nests (cells) dissected	No. nests located	No. nests (cells) dissected		
Solitary eumenid	Natural nest site	nest traps	61	61(109)	114	114(204)		
	Additional nest site	nests traps	39	39(65)	127	127(321)		
Subsocial eumenid	Natural nest site	bamboo poles	83	21(56)	254	72(186)		
	Natural nest site	nest traps	10	10(27)	28	28(72)		
	Additional nest site	nest traps	10	1(3)	55	26(69)		

reared to adulthood for identification, and then were released in the study area. This procedure gave exact survival data.

Behavior of wasps and enemies

I took data on behavioral aspects of the two eumenids (e.g. foraging time) and their enemies (e.g. methods of parasitization) by direct observations. In 1982, I observed them at the nest site No. 71 (c.f. Fig. 2) for 63 days (between 16th June to 26th September). All the following quantitative data are taken from this observation.

Comparison of parameters

In the text, I compared parameters by two test methods: 2-tailed test with normal approximation for the comparison of percentages and 2-tailed t-test for the comparison of mean values.

RESULTS

Mortality factors

Nine mortality factors, consisting of 6 parasitoid and 3 predator species, were detected by the dissection of nests of the solitary eumenid *A. flavomarginatum* (Table 2). The behavior of some parasitoids and predators are shown below briefly to facilitate an understanding of differences of mortality between the solitary and subsocial eumenids.

In egg stage, predation of a phorid fly, *Megaselia* sp. was the only distinct mortality factor for the solitary eumenid. The female phorid fly (1–2 mm in body length) searched for and located a wasp nest, entered the cell being provisioned, and sucked the wasp's egg. Then the female fly laid eggs in the cell. After hatching, the fly larvae fed on the lepidopterous larvae in the cell, then moved to the outer cells. As a result, usually all of the cells outside the attacked cell were also destroyed. The other mortality factor in the egg stage was 'failure at hatch'. This factor may be due to several causes such as overheating, disease, internal failure, etc. These causes cannot be distinguished from each

Table 2. The life tables of the solitary eumenid *A. flavomarginatum* at natural nest sites and at additional nest sites. *S* refers to the survival rate within *x*.

<i>x</i> (developmental stage)	$d_x F$ (mortality factor)	natural nest sites (nest traps)				additional nest sites (nest traps)			
		l_x	d_x	100 qx	<i>S</i>	l_x	d_x	100 qx	<i>S</i>
Eggs		204				321			
	Failure at hatch						1	0.3	
	<i>Megaselia</i> sp.		44	21.6			35	10.9	
			44	21.6	0.784		36	11.2	0.888
Larvae		160				285			
	<i>Amobia distorta</i>		32	20.0			74	26.0	
	a sp. of Formicidae		1	0.6			9	3.2	
	a sp. of Chrysididae						1	0.4	
	<i>Acroricnus ambulador</i>		2	1.3					
	<i>Campoplex</i> sp.		2	1.3			8	2.8	
	Endogenous death		5	3.1			10	3.5	
			42	26.3	0.738		102	35.8	0.642
Prepupae		118				183			
	<i>Melittobia</i> sp.		5	4.2			5	2.7	
	<i>Macrosiagon nasutum</i>						1	0.5	
	a sp. of Dermestidae						1	0.5	
	Endogenous death		6	5.1			13	7.1	
			11	9.3	0.907		20	10.9	0.891
Pupae		107				163			
	Endogenous death						2	1.2	
	Failure at emergence		6	5.6			16	9.8	
			6	5.6	0.944		18	11.0	0.890
Emerged adults		101 (49.5%)				145 (45.2%)			

other.

In larval stage, the miltogrammine fly, *Amobia distorta* ALLEN, was a major mortality factor. The miltogrammine fly was originally cleptoparasitic, but its larvae often killed the host larvae. The female miltogrammine fly found the wasp nest by following the foraging wasp as it returned to its nest. After waiting for a wasp to leave on the next foraging trip, the miltogrammine fly slipped into the cell to larviposit. The fly larvae usually pupated in the outer-most cell like the phorid fly larvae. Ant predation occurred only when the cell wall was destroyed or damaged by physical causes. I have no information on how the chrysidid parasitoid wasp attacks its host. The ichneumonid parasitoid wasp *Acroricnus ambulator* SMITH attacked the complete nest, of which the outer-most cell was closed, by thrusting its long ovipositor through some crevices in the mud wall. The larvae of the ichneumonid parasitoid wasp fed on the mature host larvae. In ten cases, larvae of the solitary eumenid died because the mother wasps had provisioned them with the lepidopterous larvae that had been parasitized by another Ichneumonid parasitoid wasp *Campoplex* sp. *Campoplex* sp. larvae often grew faster than their host larvae and thus outcompeted them. I categorized larval infections by pathogens that

Table 3. The life tables of the second generation of the subsocial eumenid *O. drewseni* at natural nest sites and at additional nest sites.

x (developmental stage)	$d_x F$ (mortality factor)	natural nest sites								additional nest sites			
		(bamboo poles)				(nest traps)				(nest traps)			
		l_x	d_x	$100 qx$	S	l_x	d_x	$100 qx$	S	l_x	d_x	$100 qx$	S
Eggs		186				72				69			
	Failure at hatch		2	1.1						3	4.3		
	<i>Megaselia</i> sp.		3	1.6						2	2.9		
			5	2.7	0.973	0	0.0	1.000		5	7.2	0.928	
Larvae		181				72				64			
	<i>Amobia distorta</i>		39	21.5		3	4.2			8	12.5		
	a sp. of Chrysididae		1	0.6									
	<i>Acroricnus ambulator</i>		3	1.7									
	Endogenous death		5	2.8		5	6.9			3	4.7		
			48	26.5	0.735	8	11.1	0.889		11	17.2	0.828	
Prepupae		133				64				53			
	<i>Anthrax</i> sp.		5	3.8		1	1.6			2	3.8		
	<i>Macrosiagon nasutum</i>		14	10.5		7	10.9			4	7.5		
	a sp. of Dermestidae					2	3.1			5	9.4		
	Endogenous death		23	17.3		13	20.3			12	22.6		
			42	31.6	0.684	23	35.9	0.641		23	43.4	0.566	
Pupae		91				41				30			
	Endogenous death		1	1.1									
	Failure at emergence		22	24.2		4	9.8			6	20.0		
			23	25.3	0.758	4	9.8	0.902		6	20.0	0.800	
Emerged adults		68 (36.6%)				37 (51.4%)				24 (34.8%)			

had entered the cell during building or provisioning, or other internal failures of developing wasp larvae as 'endogenous death'.

In prepupal stage, the eulophid wasp *Melittobia* sp., which was a general parasitoid for many other solitary wasps, bored a hole on the mud walls of the wasp nest, sucked the body fluids of the host prepupa and oviposited in the cell (IWATA, 1975). This suck by the female eulophid wasp prevented the host prepupa from pupating. But on the other hand, the eulophid larvae could not feed on the host prepupa because the skin of the host prepupa was too hard for them. Therefore, the parasitoid's attack against this solitary wasp might be an inappropriate selection of a host. The rhipiphorid beetle, *Macrosiagon nasutum* THUNBERG may probably lay many eggs in flowers (IWATA, 1975). The hatched beetle larvae are transported into the wasp nest by attaching themselves to the host wasp when the wasp visits on flowers (IWATA, 1975). At the wasp's nest, the rhipiphorid beetle larvae fed partly on mature host larvae but mainly on prepupae. The dermestid beetle larvae also fed on host prepupae.

In pupal stage, some wasps did not emerge from the pupal exuvia ('failure at emergence'). There were no parasitoids and predators recorded in this stage.

Seven mortality factors were found in the subsocial eumenid *O. drewseni* (Table 3). Six factors (4 parasitoids and 2 predators) were common to the solitary eumenid. The mortality factor not common to the solitary eumenid was the parasitoid bee-fly, *Anthrax* sp. The small first instar larvae of the bee-fly creep into the cell to attack the prepupa of the subsocial eumenid (IWATA, 1975). The mortality factors that were unique to the solitary eumenid were a species of Formicidae, the ichneumonid wasp *Campoplex* sp. and the eulophid wasp, *Melittobia* sp.

Mortality differences between the two eumenids

In egg stage, the phorid fly *Megaselia* sp. was the major mortality factor for the solitary eumenid (Table 2) while it was a minor factor for the subsocial eumenid (Table 3). The mortality by the phorid fly was significantly lower in the subsocial eumenid than in the solitary eumenid at nest traps in natural nest sites (0.0% vs 21.6%, $p < 0.01$), and at nest traps in additional nest sites (2.9% vs 10.9%, $p < 0.05$). As I discuss later, this lower mortality of the subsocial eumenid seemed to be the result of advanced maternal care. Failure at hatch was a minor mortality factor for both eumenids.

In larval stage, the miltogrammine fly *A. distorta* was a major mortality factor for the two eumenids (Tables 2 and 3). But, the miltogrammine mortality of the subsocial eumenid was significantly lower than that of the solitary eumenid at nest traps in natural nest sites (4.2% vs 20.0%, $p < 0.01$) and at nest traps in additional nest sites (12.5% vs 26.0%, $p < 0.05$). As I discuss later, the maternal care of the subsocial eumenid again reduced attacks of the miltogrammine fly. Females of the miltogrammine fly, as well as the phorid fly, seemed not to be prevented from entering the wasp nest by any characteristics of the nest structure, e.g. the entrance tube of the subsocial eumenid. Mortalities due to the chrysidid parasitoid wasp, the ichneumonid parasitoid wasp

(*A. ambulator*), and endogenous death were all negligibly small for the two eumenids. Ant predation and parasitism by the ichneumonid wasp *Campoplex* sp. sometimes occurred in the solitary eumenid.

In prepupal stage, endogenous mortality was high in the subsocial eumenid while it was low in the solitary eumenid (Table 2 and 3). The endogenous mortality of the subsocial eumenid was significantly higher than that of the solitary eumenid at nest traps in natural and additional nest sites (21.4% vs 6.3%, $p < 0.01$). It might be possible that this difference is caused by the adverse effect of the parthenogenetic reproduction by the subsocial eumenid. The lower hatchability in parthenogenetic species compared to its bisexual relatives has been known (e.g. BERGERARD, 1958, cited by TSURUSAKI, 1983; ROTH, 1974). Mortality due to the rhipiphorid beetle *M. nasutum* was also higher in the subsocial eumenid than in the solitary eumenid at nest traps in natural nest sites (10.9% vs 0.0%, $p < 0.01$) and at nest traps in additional nest sites (7.5% vs 0.5%, $p < 0.01$). This difference may be due to the higher frequency of flower visits of the subsocial eumenid. The mortality effects by the dermestid beetles were minor in both eumenids. The *Melittobia* parasitism occurred only in the solitary eumenid, and the *Anthrax* parasitism occurred only in the subsocial eumenid, but both were low.

In pupal stage, failure at emergence occurred often in the two eumenids (Tables 2 and 3), and the difference in mortality between the two eumenids was not significant (5.6% vs 9.8%, $p > 0.3$, at nest traps in natural nest sites and 9.8% vs 20.0%, $p > 0.1$, at nest traps in additional nest sites). Endogenous death was negligible in the two eumenids.

As mentioned above, the subsocial eumenid had fewer attacks of the phorid fly in egg stage and of the miltogrammine fly in larval stage, but was affected by endogenous death and attacks of the rhipiphorid beetle in prepupal stage. On the other hand, the solitary eumenid was often attacked by the phorid and miltogrammine flies but rarely

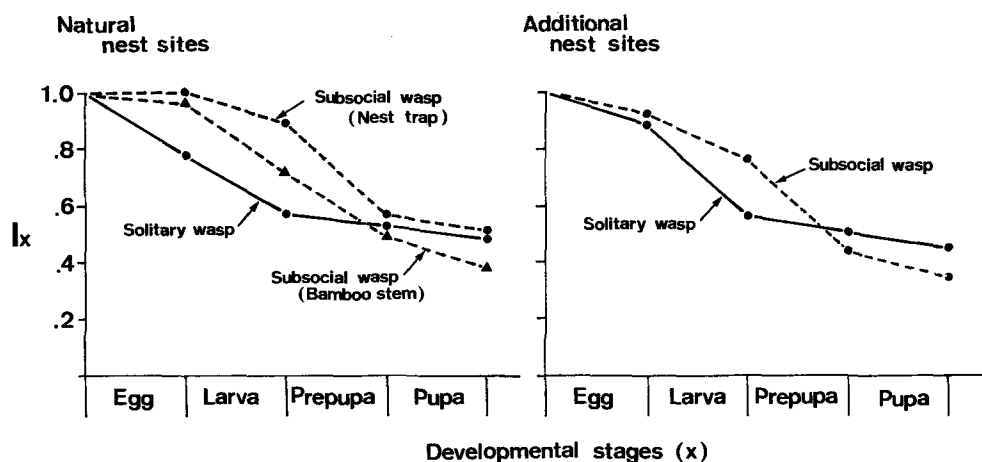


Fig. 3. Survivorship curves (l_x) of the solitary eumenid wasp *A. flavomarginatum* (solid line) and of the second generation of the subsocial eumenid wasp *O. drewseni* (dashed line) at natural nest sites and at additional nest sites. See text for the duration of each developmental stage.

failed in pupation. As a result of the counter balance of mortality among developmental stages, the percentages of emergence were nearly the same in the two eumenids (Fig. 3). The survivorship curves of the two eumenids showed the different mortality patterns between natural and additional nest sites (Fig. 3), of which the reasons will be shown below.

Mortality differences among nest sites

Bamboo poles stored at natural nest sites had been used by the subsocial eumenid before the census. During the census, the bamboo poles and nest traps at natural nest sites were continuously available for both subsocial and solitary eumenids. These stable, long continuing natural nest sites were also available for parasitoids and predators. On the other hand, nest traps at additional nest sites were unpredictable for both the eumenid wasps and their parasitoids and predators because they were available mostly for only one year. Below I will analyze the effects of this difference in nest site persistence on mortality differences.

The phorid fly *Megaselia* sp. attacked the solitary eumenid significantly more often at natural nest sites than at additional nest sites (21.6% vs 10.9% at nest traps, $p < 0.01$, Table 2). This is because the phorid flies that emerged from the natural nest sites easily found hosts there without the wide range searching, which should be done for newly made additional nest sites. In contrast, the subsocial eumenid nearly completely avoided attacks of the phorid fly even in natural nest sites (Table 3).

Mortality due to the miltogrammine fly in the solitary eumenid was not significantly different ($p > 0.1$) between nest traps in natural nest sites (20.0%) and those in additional nest sites (26.0%) as is shown in Table 2. This was also true in the subsocial eumenid (4.2% vs 12.5%, $p > 0.05$, Table 3). This can be explained by the host searching behavior of the miltogrammine fly. As already mentioned, this fly followed wasps returning to the nest. Hence, the attack rate of this fly was proportional to the frequency of foraging trips (ITINO, unpubl.). Moreover, once finding a nest, the miltogrammine fly often attacked nearby nests. Thus, the attack rate by this fly was higher at the nest sites where more hosts were nesting (ITINO, unpubl.). The absence of mortality differences can be explained, therefore, by the absence of difference in the host density between nest traps in natural nest sites and those in additional nest sites (5.0 ± 5.0 S.D. per year, $N=28$ vs 6.9 ± 5.1 , $N=26$, $p > 0.1$). As for the subsocial eumenid in natural nest sites, the attack rate was significantly higher ($p < 0.01$) at bamboo poles (21.5%) than at nest traps (4.2%), reflecting, although not proportionally, higher host density at the former (12.7 ± 8.3 , $N=20$) than that at the latter (5.0 ± 5.0 , $N=28$). Such behavioral aggregative responses in searching have been observed in several other parasitoids (HASSELL, 1968; HASSELL and MAY, 1974).

The incidence of rhipiphorid beetle (*M. nasutum*) attacks of the subsocial eumenid was not significantly different between nest traps in natural nest sites and those in additional nest sites (10.9% vs 7.5%, $p > 0.5$). In natural nest sites, there was no difference

between bamboo poles and nest traps (10.5% vs 10.9%, $p > 0.9$). This is because, unlike the miltogrammine fly, this beetle has no behavioral aggregative response.

DISCUSSION

In the solitary eumenid, *Anterhynchium flavomarginatum*, IWATA (1938a) reported four enemy species, *Pseudoxenos iwatai* ESAKI (Stylopidae), *Macrosiagon nasutum* THUNBERG, a miltogrammine fly, and a phorid fly. The latter three species were also found in this study. In 1983 one stylopid species parasitized 8% of emerged adults of the solitary eumenid. The other 6 mortality factors found in this study were not reported by him: a species of Formicidae, a species of Chrysididae, *A. ambulator*, *Campoplex* sp., *Melittobia* sp. and a species of Dermestidae.

In the subsocial eumenid, *Orancistrocerus drewseni* (*Ancistrocerus fucaianus* SCHULTHESS in his paper), IWATA (1938b) found five enemy species, *Anthrax distigma* WIEDEMANN (*Argyromoeba distigma* WIEDEMANN), *Acroricinus ambulator* SMITH, *Macrosiagon nasutum* THUNBERG, a eulophid wasp and a miltogrammine fly. In the present study, I detected four of them except the eulophid wasp. *Anthrax* sp. in Table 3 may be *A. distigma*, but the identification is not clear at present knowledge (HISAMATSU, pers. comm.). *Megaselia* sp., a species of Chrysididae and a species of Dermestidae were not found in IWATA (1938b).

Egg mortality due to the phorid fly *Megaselia* sp. was lower in the subsocial eumenid than in the solitary eumenid. The subsocial eumenid wasp progressively provisions her progeny for 6–9 days, during which it spends much of time in the nest checking the contents of the cell. When the phorid fly invaded the nest, it was often found and driven away before sucking the host egg (ITINO, unpubl.). Even when one cell was attacked and the wasp egg was sucked, the subsocial eumenid wasp immediately deserted that cell after isolating it with mud. Such muddy shields were observed 5 times (Table 3). Thus the maternal care by the subsocial eumenid wasp against the phorid fly consisted of checking the cell contents and the isolation of attacked cells.

Larval mortality due to the miltogrammine fly was also lower in the subsocial eumenid than in the solitary eumenid. The reason for the difference appears to be as follows. The foraging time for prey of the subsocial eumenid (including the successful and unsuccessful foraging trip) was longer than that of the solitary eumenid (80.1 ± 60.7 min, $N=883$ vs. 30.2 ± 27.4 , $N=87$, $p < 0.005$) though the detailed data will be given in ITINO (unpubl.). And the staying time between the two consecutive foraging flights was also longer in the subsocial eumenid than in the solitary eumenid (8.7 ± 19.7 min, $N=909$ vs. 2.7 ± 3.5 , $N=81$, $p < 0.005$). The longer foraging time and the longer staying time reduce the risks to be invaded by the miltogrammine fly in two ways. First, as mentioned in the results, when the host wasp leaves the nest, the fly tries to slip into the nest. But, when the fly failed in this trial, it remains in front of the nest for up to several dozen minutes waiting for the next return of the host wasp (ITINO, unpubl.).

Thus, the longer the foraging duration is, the less the nest of the wasp is attacked by the waiting fly. Secondly, attacks by the miltogrammine fly are successful mainly when the host wasp leaves its nest within a few minutes after its previous return (ITINO, unpubl.). Thus, the longer staying time of the subsocial eumenid reduces the chances of the miltogrammine fly to invade the nest. Moreover, the female subsocial eumenid frequently inspected her brood cell. Thus, it is possible that she could find the fly larvae and kill them. IWATA (1975) showed, in another subsocial eumenid *Pararrhynchium ornatum* SMITH, that the female wasp bit the larvae of the miltogrammine fly *Amobia distorta* that invaded the brood cell.

By removing the mother from her eggs and/or larvae, EBERHARD (1975), SAKAGAMI and MAETA (1977), and TALLAMY and DENNO (1981) have tested the effectiveness of maternal care. This paper employs another method of assessing the effect of maternal care; comparison of mortalities between two closely related, cohabiting wasps and between two different types of nest sites. This method permits me to clarify the ecological factors that favor maternal care. As described in the results, the phorid fly attacked nests near their birth place, while the miltogrammine fly followed returning host wasps to locate their nest sites. The attack rates of these enemies were, therefore, higher at the persistent nest sites with high host density. This is consistent with suggestion that anti-enemy defense behavior of wasps and bees is important especially when they live in an aggregation of nests (EVANS, 1977; BROCKMANN, 1984). In such situations, host wasps and bees may have some defense mechanisms against the enemies; the communal or semisocial nesting (MICHENER, 1974), the accessory burrows (TSUNEKI, 1963), or the presence of male at the nest entrance (PECKHAM, 1977). ENDO (1980) showed that the anti-parasite response at each nesting process of a solitary spider wasp improved the nesting success of the wasp. In this study, maternal care (subsociability) appears to be an effective defense mechanism. The adaptiveness of subsociability in Hymenoptera has been supported circumstantially in a *Bembix* wasp (EVANS, 1966) and documented directly in two *Ceratina* bees (SAKAGAMI and MAETA, 1977).

WHEELER (1923) proposed the hypothesis that trophallaxis promoted the direct contact between mother and larvae, and that the larval attractiveness somehow facilitated group life through subsociability to eusociality. Certainly trophallaxis is often observed in eusocial wasps. In *Vespa orientalis*, larval secretions are essential to the protein digestion of adults (IKAN et al., 1968). In subsocial wasps, however, trophallaxis is unreported (IWATA, 1942). It appears that trophallaxis is not the only requisite for the evolution of subsociability in wasps. There might be several possible routes through which subsocial behavior evolved. My results support the idea that the selective pressure by enemies is one of the responsible factors for the origin of subsociability in wasps.

SUMMARY

I compared life tables between the solitary eumenid wasp *Anterhynchium flavomarginatum*

SMITH and the subsocial eumenid wasp *Orancistrocerus drewseni* SAUSSURE in Kyoto, Japan, during 1980–1983. The subsocial eumenid is parthenogenetic in this study area. There were 9 identified mortality factors in the solitary eumenid and 7 in the subsocial eumenid, 6 of which were common to the two eumenids. The important differences of mortality between the two eumenids were seen in the egg, larval, and prepupal stages. In the egg stage, mortality by the phorid fly *Megaselia* sp. was much lower in the subsocial eumenid (1.4%) than in the solitary eumenid (15.0%) likely because of the maternal care of the subsocial eumenid (progressive provisioning and other related behavior), which reduced predation pressure. In the larval stage, mortality by the miltogrammine fly *Amobia distorta* was also lower in the subsocial eumenid (8.1%) than in the solitary eumenid (23.8%) also probably because of the maternal care of the subsocial eumenid. A comparison of mortality in the two eumenids between the stable, long continuing natural nest sites and the additional temporal ones showed that the phorid fly remained near its birth place and parasitized stable nest sites. The miltogrammine fly followed returning eumenid wasps and parasitized those nest sites that have a high host density. In the prepupal stage, mortality by endogenous death was higher in the subsocial eumenid than in the solitary eumenid. Mortality due to the rhipiphorid beetle was also higher in the subsocial eumenid probably due to more frequent flower-visits by the subsocial eumenid.

The defense mechanism of the subsocial eumenid was discussed in relation to the evolution of subsociality.

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単独性のオオフトオビドロバチと亜社会性のオオカバフスジドロバチの
母親による子の保護の適応的意義を評価するための生命表の比較

市野隆雄

京都市において、単独性のカリバチであるオオフトオビドロバチ *Anterhynchium flavomarginatum* と亜社会性のオオカバフスジドロバチ *Orancistrocerus drewseni* の野外調査を、1980年から1983年まで行い、生命表を種間で比較した。この調査地においては亜社会性ドロバチは単為生殖を行っている。単独性ドロバチでは、9つの、亜社会性ドロバチでは7つの死亡要因が識別できたが、そのうち6つは両種に共通のものであった。2種間の死亡率の大きな違いは卵期と幼虫期と前蛹期にみられた。卵期にはノミバエの1種が両種ドロバチの卵を捕食したが、これによる死亡率は単独性ドロバチ (15.0%) よりも亜社会性ドロバチ (1.4%) のほうがはるかに低かった。これは亜社会性ドロバチの母親による保護 (随時給食とそれに関連する諸行動) が捕食の機会を減少させたためと考えられた。幼虫期にはニクバエの1種 *Amobia distorta* の捕食寄生率が、やはり単独性ドロバチ (23.8%) よりも亜社会性ドロバチ (8.1%) で低かったが、これも亜社会性ドロバチの母親による保護が原因と思われる。安定で永続的な環境である自然営巣場所と一時的な環境である付加営巣場所で2種のドロバチの死亡率を比較したところ、ノミバエは羽化場所付近にとどまって産卵するため、永続的な営巣場所のほうが捕食率が高いことがわかった。また、ニクバエは帰巣するドロバチを追跡することにより巣を発見し、また一度発見すると次々とまわりの巣を攻撃するので、営巣密度の高い営巣場所での捕食寄生率がより高かった。前蛹期には不明死亡率が単独性ドロバチよりも亜社会性ドロバチで高かった。これは単為生殖の悪影響と推定される。ハナノミによる死亡も亜社会性ドロバチのほうが多かったが、これは亜社会性ドロバチのほうがより頻繁に訪花するためであると思われる。

亜社会性ドロバチの防衛機構について亜社会性の進化と関連づけて論議した。