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Bionomics of *Elasmus japonicus* (Hymenoptera, Elasmidae), a Parasitoid of a Paper Wasp, *Polistes snelleni* (Hymenoptera, Vespidae)

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Abstract A parasitic wasp, *Elasmus japonicus*, frequently infested pre-emergence and post-emergence nests of *Polistes snelleni*. It had at least two generations a year. Adults of the overwintering generation mainly attacked nests of *P. snelleni* during the pre-emergence stage, and adults of the later generation(s) attacked post-emergence nests. Larvae of the parasitoid externally fed on host immatures which had already spun cocoon. Mature larvae communally made fecal partitions in the cell before pupation to separate themselves from the host remnants. Workers and foundresses of *P. snelleni* usually removed cocoon caps of infested cells after the fecal partition was completed, though they sometimes killed the parasitoid larvae before that. Twenty to 29% of pre-emergence nests were parasitized by *E. japonicus*, and the loss in the number of workers owing to the parasitoid was estimated at 18 to 35% in three years. Parasitism levels reached 73 to 92% in post-emergence nests, which lost 17 to 22% of reproductives because of the parasitoid. Individual infested cells had means of 23 to 27 pupae of the parasitoid, with the sex ratio (proportion of males) varying from 0.04 to 0.75, though highly female-biased in most cells.

Key words: *Polistes snelleni*, *Elasmus japonicus*, social wasp, parasitoid, colonial productivity, natural enemy.

Introduction

Eusocial wasps lose their larvae or pupae to many parasitoids despite their apparent vigilance over natural enemies. *Polistes*, one of the most studied groups for biology among the eusocial wasps, has over 40 recorded parasitoid species, mainly of Hymenoptera, Lepidoptera and Diptera (MAKINO, 1985). Some parasitoids can cause considerable losses in worker force or reproductive output in colonies of the hosts (MAKINO, 1989).

Wasps of the genus *Elasmus* of Elasmidae are mainly either primary external parasitoides of larvae of Lepidoptera or hyperparasitoids upon them through various Hymenoptera, particularly Ichneumonidae and Braconidae (CLAUSEN, 1940). However, five species (*E. schmitti*, *E. biroi*, *E. lamborni*, *E. polistis*, and *E. japonicus*) are recorded as primary parasitoids of *Polistes* (BURKS, 1971). Of these, *E. polistis* of North America has been studied for its biology (NELSON, 1976; REED and VINSON,

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1979; STRASSMANN, 1981). Although *E. japonicus* is recorded from *Polistes* in Japan (TACHIKAWA, 1965; IWATA and TACHIKAWA, 1966; MAKINO, 1983), there is no biological information except for a brief account on the number of parasitoid pupae per cell by IWATA and TACHIKAWA (1966). In the course of an ecological study of *Polistes snelleni*, we have noticed that the nests are frequently infested with *E. japonicus*. We describe some bionomic observations of the parasitoid, its infestation level, and the extent to which the host nests lost adult productivity because of the parasitism.

Materials and Methods

The study was made in Misumai and Toyotaki (about 2 km apart from each other), Sapporo (43°N, 141°E), Japan in 1980–1982 and in 1989–1991. The study fields were in grassy patches scattered with young trees, such as willows, birches or alders near the Toyohira River. *P. snelleni* predominantly nested on twigs of these trees (MAKINO and SAYAMA, 1991), and less frequently on dead stems of herbaceous plants. Another paper wasp, *P. riparius*, also inhabited the fields, but *E. japonicus* infested it only very rarely. The principal parasitoid of *P. riparius* was an ichneumonid, *Latibulus* sp. (MAKINO, 1983, 1989), which sometimes parasitized *P. snelleni* (SAYAMA and MAKINO, unpublished data).

In the fall (late August to October) and/or spring (April to early May) in 1980–1982, we collected nests of *P. snelleni* in the study fields of Toyotaki and Misumai, and along a path connecting the two localities after all adults had left the nests. Cells infested with *E. japonicus* were easily recognized, because they had brown fecal partitions inside. The partitions were made by larvae of the parasitioid before their pupation to separate themselves from host remnants, as is reported in *E. polistis* (REED and VINSON, 1979). The infested cells either contained pupae of *E. japonicus*, or had small holes on the wall from which adults of the parasitoid had gone outside. When the pupae were contained, they were counted for each cell. In 1981 and 1982, sexes of the pupae were identified by the length of antennae, which were longer in male. In 1989–1991, initiated nests of *P. snelleni* were marked in May in Misumai, and brood maps were regularly made for them. Emerged adults were marked to determine the number of adults produced from each nest. Parasitized cells, which were recognized as above, were recorded on the maps when noticed. Behavior of adults of the parasitoid was observed when we found them near or on nests of the host.

Immatures of a colony were divided into two categories in a way similar to that of MAKINO (1989): foundress-reared brood (FRB) and worker-reared brood (WRB). FRB was composed of individuals that spun cocoon during the pre-emergence stage, and their number was referred to as "FRB size." FRB size was the number of adults to be reared by the foundress alone. WRB was individuals that spun cocoon during the post-emergence stage, and their total number was WRB size.

Results and Discussion

1. *Life cycle*

Elasmus japonicus had at least two generations a year. It overwintered as pupa in the nest of *P. snelleni*. It is unknown when *E. japonicus* eclosed and went outside the nest, though the eclosion was not earlier than early May, because infested nests collected in early May still had pupae of the parasitoid. We began to see adults of *E. japonicus* near nests of *P. snelleni* in mid to late June when average nests had the first cocoons of FRB (SAYAMA, unpublished). Then, *E. japonicus* seems to attack hosts after cocooning of the latter as does *E. polistis* (REED and VINSON, 1979). Fecal partitions of the parasitoid began to appear in early July when only a small fraction of nests had adult workers. Thus, the adult parasitoid of the overwintering generation presumably finished attacking pre-emergence nests by early July.

We saw adults of *E. japonicus* more frequently from early August on, that is, during the late post-emergence stage. Probably these adults were of the last generation, and eggs laid by them would produce the overwintering pupae. Whether or not there was another generation between the first and the last is unknown. The generation time from egg to adult is about 25 days in *E. polistis* (REED and VINSON, 1979). If *E. japonicus* has a similar developmental time, eggs laid in late June will produce adults of the second generation in mid to late July, and the assumed third-generation adults will appear in mid to late August when we found adults of the last generation in the field. Thus, it is possible that *E. japonicus* has three generations a year, and the possibility is larger in central to southern Japan, where nesting period of *P. snelleni* is longer than in Hokkaido (MAKINO, personal observation).

We obtained secondary parasitoids, *Pediobius* spp. including *P. crassicornis* (Eulophidae), from 5 of 59 (9%) nests studied in 1989–1991. They emerged from overwintering pupae of *E. japonicus* which were kept under room temperatures.

2. *Adult behavior of the parasitoid toward the host nests*

Adults of *E. japonicus* were often found sitting on leaves or twigs near nests of *P. snelleni* (Fig. 1). For example, we saw one or more adults of the parasitoid near five out of seven nests censused in the afternoon of August 22, 1980. They often flew swiftly around the nest in a zigzag manner and sometimes alighted on it. Some directly jumped on the comb from the place near the nest. Workers of *P. snelleni* that found *E. japonicus* on the nest fluttered the wings and darted about on the comb. This behavior was similar to that of *P. riparius* workers when they found an ichneumonid, *Latibulus* sp., on or near their nest (MAKINO, 1983). Once we saw a *P. snelleni* worker bite and kill *E. japonicus* that sneaked into the nest.

Fecal partitions were usually exposed in parasitized cells, showing that wasps of *P. snelleni* recognized those cells and removed cocoon caps and host remnants after the partitions were completed. Removal of cocoon caps of parasitized cells also occurs in *P. fuscatus* (REED and VINSON, 1979). Once completed, the partitions

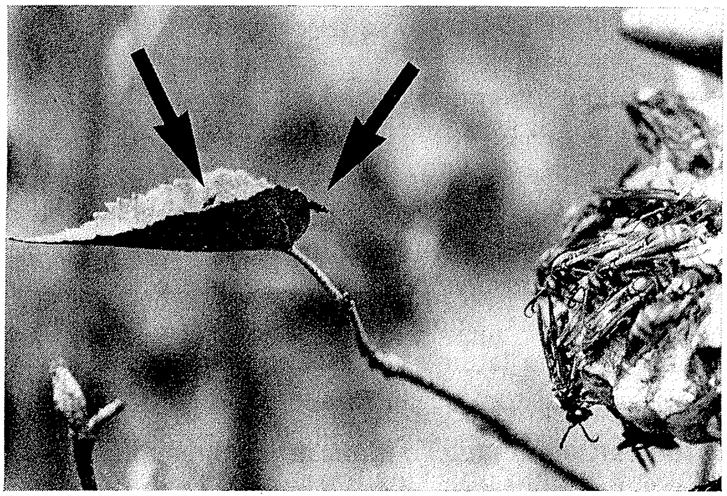

Fig. 1. *Elasmus japonicus* adults (arrows) sitting on a leaf near a nest of *Polistes snelleni*.

were not broken and the contained pupae were not killed by *P. snelleni*. In a few cases, however, we saw a *P. snelleni* worker devour larvae of *E. japonicus* before the latter made the fecal partition. Thus, at least under some conditions, *P. snelleni* were able to detect the parasitoid larvae and/or parasitized hosts under cocoon caps before the partition was made. To avoid detection during host feeding is important to the survival of *E. polistis*. From the viewpoint of *P. snelleni*, to kill the parasitoid larvae may be beneficial, if emerged adults of *E. japonicus* tend to reparasitize the nest, as reported in *E. polistis* (STRASSMANN, 1981). Further study is interesting to reveal how the host detects the parasitoid larvae before they make the fecal wall and how the parasitoid avoids the detection.

3. *Number of parasitoid pupae per host cell and their sex ratios*

Distances between the fecal partition and host meconium at the bottom of infested cells varied from 4 to 9 mm (n=10), roughly correlated with the number of contained pupae of *E. japonicus*. In addition to the partition, meconium of the parasitoid often covered the inner cell walls and bottom as in *E. polistis* (REED and VINSON, 1979).

The number of pupae of *E. japonicus* per infested cell ranged from 3 to 57 in the nests collected in the fall in 1980–1982 (Fig. 2). Mean number of pupae was 26.4±SD 12.2 (18 cells from 8 nests) in 1980, 26.7±11.4 (26 cells from 11 nests) in 1981, and 23.1±SD 10.4 in 1982 (46 cells from 11 nests). There was no significant difference in the mean among the years ($p>0.05$; ANOVA).

Sex ratio (proportion of males) of *E. japonicus* pupae from individual cell varied from 0.04 to 0.34 ($n=21$) in 1981 and from 0.06 to 0.75 ($n=46$) in 1982, though female-biased in most cells (Fig. 3). There was no significant correlation between the number of pupae and sex ratio in both years (KENDALL's $\tau=0.263$ in 1981; -0.123 in 1982; $p>0.05$). The female-biased sex ratio suggests that sib mating

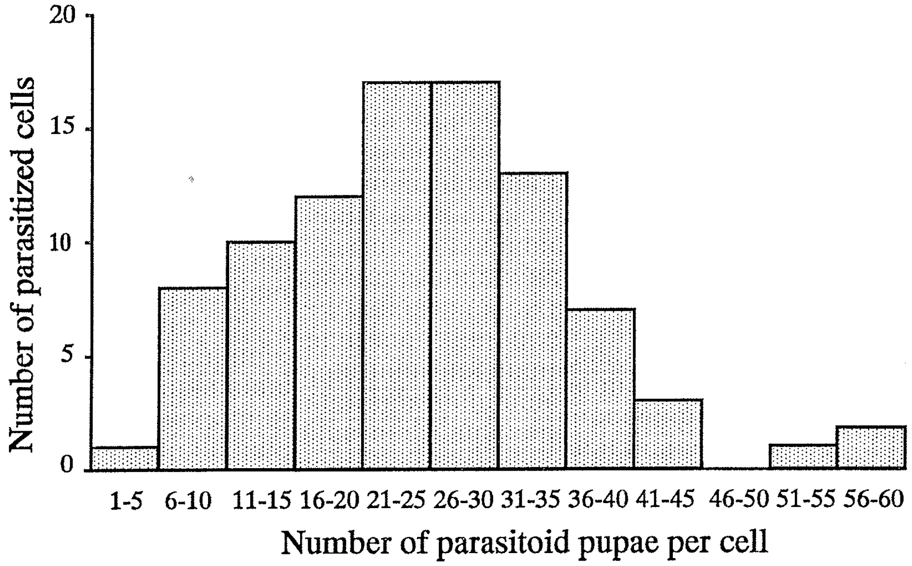

Fig. 2. Frequency distribution of the number of *Elasmus japonicus* pupae per infested cell of *Polistes snelleni*.

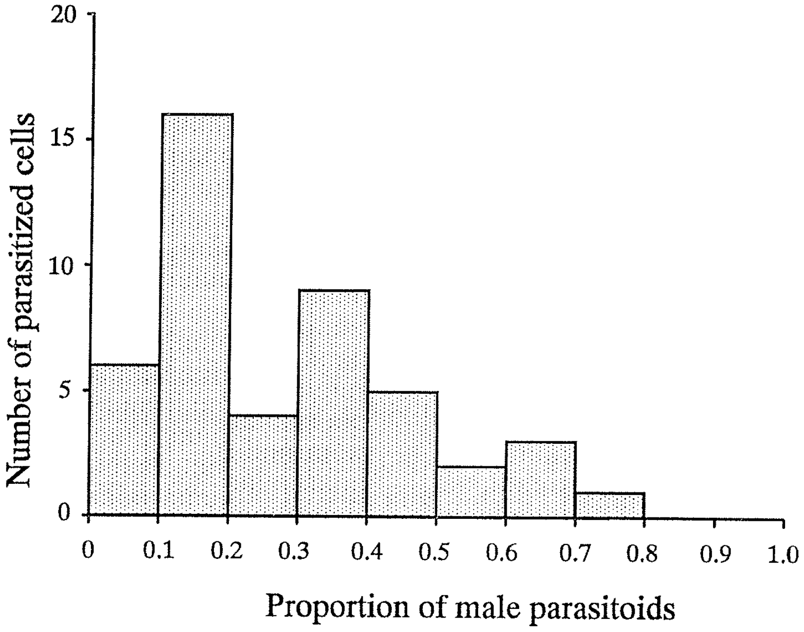

Fig. 3. Frequency distribution of sex ratio (proportion of males) of *Elasmus japonicus* pupae in individual infested cells of *Polistes snelleni*.

occurred (HAMILTON, 1967). In *E. polistis*, emerged males wait for females to emerge near the nest, making sib mating likely to occur (STRASSMANN, 1981).

4. *Levels of parasitism and losses of adults in the host*

Forty-seven to 100% out of the nests collected after adults left them had at least

Table 1. Parasitism levels of *Elasmus japonicus* in *Polistes snelleni* nests in 1980–1982. "Infested nests" had at least one cell infested with *E. japonicus*.

Locality[1]	Time of collection	Number of nests examined	% infested nests	No. meconia in infested nests (Mean±SD)	% adult loss in infested nests[2] (Mean±SD)
Toy, Mis	Fall, 1980	25	80	32.1±20.7	28.5±25.7
Toy-Mis	Spring, 1981	17	47	60.4±21.1	5.4± 4.5
Toy-Mis	Fall, 1981	7	100	57.7±19.8	19.6±18.7
Toy	Fall, 1982	11	100	64.5±30.2	11.4±13.2

1) "Toy" and "Mis" stand for Toyotaki and Misumai, respectively. "Toy-Mis" means a path connecting the two localities.

2) Calculated as: No. infested cells/No. meconia ×100.

Table 2. Parasitism levels of *Elasmus japonicus* in FRB (foundress-reared brood) and WRB (worker-reared brood) in *Polistes snelleni* nests in 1989–1991.

	FRB				WRB			
Year	No. nests ex-amined	% infested nests	FRB size[1] of infested nests (Mean±SD)	% FRB loss[1] in infested nests (Mean±SD)	No. nests ex-amined	% infested nests	WRB size[1] of infested nests (Mean±SD)	% WRB loss[1] in infested nests (Mean±SD)
1989	30	20	9.8±4.0	34.2±10.9	25	92	39.5±22.1	17.3±17.9
1990	34	29	10.4±4.3	34.7±27.5	30	87	28.3±16.5	18.5±14.6
1991	30	23	12.9±3.1	18.0±11.7	22	73	31.3±19.8	22.0±21.2

1) For explanations of FRB size, FRB loss, WRB size and WRB loss, see text.

one infested cell with the fecal partition (Table 1). Assuming that all immatures of *P. snelleni* grew into adults after excreting meconia unless parasitized by *E. japonicus*, we calculated losses in adult production due to the parasitism. The loss in adult production was 5 to 33% on average in the infested nests (Table 1).

Estimation of losses in worker and reproductive production was possible for the nests in 1989–1991. For these nests, parasitism on FRB was distinguished from that on WRB using brood maps. On the basis of the adult production schedule of *P. snelleni*, FRB was assumed to mainly produce worker adults, while WRB to produce reproductives (SAYAMA, upublished). Then, losses of FRB and WRB roughly correspond to losses of workers and reproductives, respectively. Worker loss varied from 18 to 35% and reproductive loss from 17 to 22% from year to year (Table 2).

Percent parasitism was much larger in WRB than in FRB (Table 2), which means that the nests were more frequently parasitized in the post-emergences stage than in the pre-emergence stage. This may reflect a growing population of *E. japonicus* during a year.

There was no significant correlation ($p > 0.05$) between the number of cells and the number of parasitized cells in the four samples in Table 1 (KENDALL's τ ranged from 0.05 to 0.37). Likewise, with the nests in Table 2, no correlation was found between the two variables both in cells made during the pre-emergence stage (τ ranged from -0.095 to 0.189) and those made during the post-emergence stage (-0.126 to 0.202). Thus, susceptibility to the parasitism did not increase with the nest size before or after the worker emergence. This differs from STRASSMANN's (1981) results of *E. polistis* parasitizing *P. exclamans*, though the reason for the difference is unclear.

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