

INTRASPECIFIC LARVAL COMPETITION AMONG WASPS PARASITIC OF BEAN WEEVIL LARVAE

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INTRODUCTION

Intraspecific competition has been thought to be the primary driving force of evolution since Darwin proposed the theory of natural selection. Nicholson (1954) proposed the two extreme forms of competition when individuals compete for common resources; 'scramble' type and 'contest' type competitions. The former type occurs when competing individuals have equal access to a common resource. With this mode of competition, all individuals die when the resource is used up. In 'contest' type competition, some individuals monopolize the resource, while the others are left with no resource. With this mode of competition, only those who have secured resources can survive. These modes of competitions are the two extremes, and there are many intermediate forms. However, the concept of 'scramble' and 'contest' type competitions has been very useful, both in theoretical and experimental population ecology. The concept has been especially helpful when we consider the mechanisms of population dynamics.

There are many parasitic species of Hymenoptera and Diptera which live on other insects. They are often called parasitoid. The parasitoid differs from parasite (*sensu stricto*) in that parasitoid individual(s) eventually kills the host individual. The female wasps or flies lay their egg(s) in or on other insect of various stages suitable for the development of their offspring. The former is called endoparasitic insects and the latter, ectoparasitic.

Within parasitoid wasps and flies, there are two major classes of competition among individuals in or on the host. They are gregarious and solitary. In the former species, female lays more than one egg in or on one host at one bout. Many eggs develop to adults. On the other hand, in the solitary species, female wasp usually lays one egg on a host at a time, and usually only one parasitic wasp emerges from one host.

The solitary larva consumes an entire host to complete its development. Each host represents a fixed amount of resource. Although parasitoid females have a tendency to avoid superparasitism when their resources are in ample supply, when the host resource is in short supply, superparasitism often occurs, and more than one conspecific egg are oviposited in or on one host. When more than one parasitoid larva

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are present on one host, they must fight to possess the host and all but one larva eventually die (i.e., contest type competition). When a female reencounters the host on which she oviposited before and lays egg(s) onto it, 'self superparasitism' occurs. When a female encounters a host parasitized by another conspecific female(s) and lay egg(s) on it, 'conspecific superparasitism' occurs (Van Dijken and Waage, in press; Bakker et al., 1985). Whichever type of superparasitism occurs, there usually is a time-lag between the first and subsequent oviposition(s). Also, it should be mentioned that the competition in solitary wasp can occur only during a certain period in its life time.

The elimination of the multiple larvae in solitary parasitoids has been known since the work on the biological control of insect pest began at the end of the last century. There are many experimental studies on the mechanisms of larval competition in parasitoid species (e.g., Lawrence, 1988; Chow and Mackauer, 1984). Several suggestions have been made for the possible mechanisms of competition between solitary endoparasitic species (e.g., in *Nemeritis* by Fisher, 1961). Fisher (1961) suggested the two phases of mechanisms: (1) physical attack where a parasitoid uses its mandibles to fight another, and (2) physiological suppression where the older larva continues to grow, eliminating the younger through starvation. However, most studies on larval competition dealt with endoparasitoid, and as far as we know there is no study with ectoparasitic species.

In this study, we investigated the mechanism of competition that takes place during the immature stage by employing the technique of egg transfer. Using solitary ectoparasitic wasps we focused our attention on the following two points; (1) the mechanism of conspecific larval competition (whether they are 'interference' or 'exploitation' type or some other mechanisms such as 'intraspecific predation' (cannibalism)), and (2) the effect of the relative ages of the competing larvae on the competition mechanisms and competitive outcome. Finally we discuss the mechanisms of population regulation in solitary wasp species as well.

EXPERIMENTAL ORGANISMS

Organisms

All experiments were conducted in the growth cabinet controlled at 30°C and 70% r.h. We used the three species of parasitic wasps, *Dinarmus basalis* (Rondani) (Hymenoptera: Pteromalidae), *Anisopteromalus calandrae* (Howard) (Hymenoptera: Pteromalidae), and *Heterospilus prosopidis* (Viereck) (Hymenoptera: Braconidae).

These wasps are solitary and ectoparasitic on the larvae and pupae of the azuki bean weevil, *Callosobruchus chinensis* (L.) (Coleoptera: Bruchidae), under laboratory conditions (Kariya and Kurosawa, 1939; Utida, 1943, 1944, 1948; Arora and Singh, 1970; Okamoto, 1971; Bellows, 1979). *A. calandrae* and *H. prosopidis* have been extensively used in ecological studies on population dynamics (e.g., Utida, 1953, 1955,

1957; Kistler, 1979; Fujii, 1983). Their morphological characteristics and parasitizing behaviors were described by Shimada and Fujii (1985) and Rasplus J-Y (1986). Detailed descriptions on the primary characteristics of *D. basalis* were reported by Fujii and Maeda (in manuscript).

The female wasps of *D. basalis* and *H. prosopidis* usually lay one egg per host. However, all three wasp species lay multiple eggs when the host resource is scarce relative to the female wasp density. Also all three species are often found to lay more than one egg on one host even when some unparasitized hosts were available. Thus, their ability to discriminate between parasitized and unparasitized hosts is not perfect. The ability seems much lower in *A. calandrae* than the two other species. All three wasp species preferred the late fourth instar bean weevil larvae as a host (Shimada and Fujii, 1985).

Host Stock Culture

The biology of the host species, *C. chinensis*, is well known (e.g., Utida, 1941a, b, c; Arora and Singh, 1970; Bellows, 1979; Hassell et al., 1985). In our laboratory, they are usually raised on the azuki bean, *Vigna angularis*.

The beetle cultures were set up every alternate days in ventilated glass Petri dish (120 mm in diameter, 30 mm in depth). The dish had one or two layers of azuki beans. Freshly emerged adult beetles from the stock culture were allowed to lay eggs on beans for 24 hours. This procedure assured that hosts of known age were continuously available. Only beans which contained 16-17 day old weevil larvae were used in these experiments.

Parasitoid Wasp Stock Culture

Beans which contained 16-17 day old (late fourth instar) larvae of *C. chinensis* were introduced in one layer into two compartments of a four-compartment Petri dish (Falcon No. 1009: 90 mm in diameter, 15 mm in depth). Adult parasitoids randomly chosen from the stock wasp culture three days after the first emergence were introduced and confined in the Petri dish. They were kept in the dish until their deaths. This procedure was repeated daily to obtain a continuous supply of freshly emerged parasitoids. Stock cultures of all three wasp species were maintained in the similar manner.

Observation Apparatus

We prepared acrylic plastic plates (100 mm × 55 mm × 4 mm) with 10 drilled out wells in two rows. Each well was 5mm in diameter and 4mm in depth. The late fourth instar hosts, about the size of the cavity (mean fresh weight of 7.21 mg), just fit in the wells. Each well was to represent a space made by a host larva while inside a bean. By carrying out all the experiments in the acrylic plastic wells, we were able to see the competitive process directly under the dissecting microscope during the entire

experimental period. The plate was covered by a slide glass after introduction of host and parasites.

SIMULTANEOUS INTRODUCTION OF MULTIPLE EGGS

Host Preparation

Beans containing 16-17 day old larvae were placed in a four-compartment Petri dish. About 25 randomly chosen parasitoid females of one species from stock culture were then introduced into the Petri dish. They were allowed to parasitize the hosts for 4 hours. After the parasitoid females were removed, the beans were opened immediately. Host larvae with parasitoid egg(s) on them were collected. After removing the parasitoid egg(s) from the host, the host larvae were washed in lukewarm water to remove any debris on host surface, and then dried with tissue paper. Each host larva was then transferred into a well of acrylic plastic plate. The parasitoid females are known to paralyze their host before oviposition. The above procedure assured that the transferred parasitic wasp eggs meet host conditions upon hatching similar to those experienced by a parasitoid hatching normally on a larva inside a bean.

Parasite Egg Preparation

For every replicate of the experiment, 25 three days old female wasps were randomly chosen from the stock culture. They were slightly anesthetized and kept in an empty Petri dish for one day without hosts. Depriving the females in this fashion prompted them to lay many eggs in a short period when hosts were provided. The female wasps were allowed to lay eggs on 16-17 day old hosts for 4 hours. The procedure thus minimized the difference in hatching time among eggs. The beans were opened immediately afterward and each parasitoid egg found was transferred onto a naked host larva inside a well.

Experiment

To investigate the mechanisms of competition, especially during the early larval stages of the parasitoid, we transferred 2 or 5 eggs of one wasp species onto a naked host. As a control a single egg transferal experiment was also carried out to record the percentage of offspring emergence of each wasp species without competitor. This also served as a check for any ill effects of the egg transfer treatment. Observations were made under a dissecting microscope every two hours after the egg transfer.

Results

The results are summarized in Table 1 and Fig. 1. In single egg transferal experiments, 81 to 86 transferred eggs (out of 100) emerged as adults in all three wasp species. So we can conclude that our experimental procedures (host and parasitoid egg transfers) have no large ill effects on the survival of the organisms employed. In 7

Table 1. Results of simultaneous, multiple egg transferal experiments.

| Wasp species | Experimental condition | No of parasitic wasps emerged (out of 100 hosts) | No. of host emerged | No. of dead wasp larvae found on each host | No. of dead wasp pupae found on each host |
|----------------------|------------------------|--|---------------------|--|---|
| <i>D. basalis</i> | 1 egg/host | 86 | 7 | 5 | 2 |
| | 2 eggs/host | 86 | 1 | 13 | 0 |
| | 5 eggs/host | 83 | 14 | 3 | 0 |
| <i>A. calandrae</i> | 1 egg/host | 81 | 7 | 7 | 2 |
| | 2 eggs/host | 89 | 9 | 0 | 2 |
| | 5 eggs/host | 92* | 15 | 0 | 0 |
| <i>H. prosopidis</i> | 1 egg/host | 83 | 11 | 6 | 0 |
| | 2 eggs/host | 89 | 7 | 4 | 0 |
| | 5 eggs/host | 87 | 4 | 8 | 1 |

*Two wasps emerged from one host in 7 cases.

cases in both *D. basalis* and *A. calandrae*, and 11 cases in *H. prosopidis*, the host larvae successfully emerged as adult. In these cases, we found no remains of the parasitoid larva. This suggests that the parasitoid egg did not hatch, or that the parasitoid larva died at very early stage. This also suggests that the host-paralization by wasp female before oviposition is not always effective. Table 1 also shows the numbers of dead wasp larvae and pupae found on the host body.

In 2 and 5 eggs transferal experiments, 83 to 92 wasp offspring could emerge as adults from 100 hosts in all three species. Only in 7 cases of *A. calandrae* in 5 egg transferal experiment, 2 offspring emerged from one host. This result shows that the 16-17 day old host, in terms of amount of resources, can support the development of at least 2 larvae of *A. calandrae*.

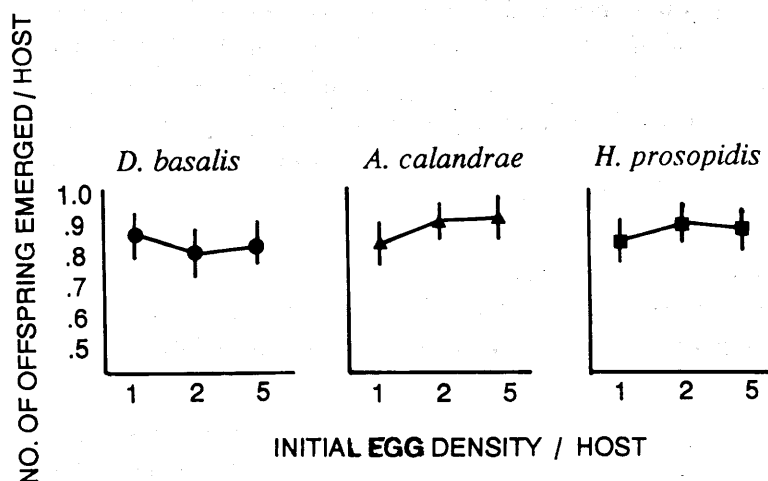


Fig. 1. Mean number of offspring emerged per host in simultaneous egg introduction experiment. The vertical bar shows the 95% confidence interval of the mean. Abscissa shows the initial egg density per host.

Detailed observations on multiple wasp eggs on one host revealed the following behavior. Larva after hatching moved a short distance from the egg shell and then fed on the host for several minutes. Then, the larva actively moved around for few hours. The active larva punctured the unhatched eggs and bit newly hatched larvae when first encountering them. The time required to puncture an egg or to overcome a rival larva was about 30 to 45 minutes. After a larva had overcome all the eggs and other larvae on the host, it continued to move around for few more hours before settling down to exploit the host resource. No preference for a specific exploitation site on the host body was found in any of the three wasp species.

TIME-LAG INTRODUCTION OF TWO EGGS ON ONE HOST

In this experiment, we tried to determine the effect of different arrival times of two eggs on the same host on their intraspecific competition. We transferred two eggs of the same parasitoid species onto one host with a predetermined time-lag. In the following, we call the egg introduced first the occupant, and the second egg the invader.

Methods

The hosts were prepared as in the simultaneous introduction experiment. Hosts were always 16–17 days old when the occupant egg was introduced.

We used the time-lags of 24, 48, 72, and 96 hours. All three wasp species used in this experiments became prepupa by 96 hours, so larger time-lags were unnecessary.

We first introduced one parasitoid egg of a species onto a naked host in a well, as done for controls in the simultaneous introduction experiment. After 24, 48, 72, or 96 hours, another egg of the same species was introduced on the same host. Initially, one hundred replicates were prepared for each time-lag period of each parasitoid species. However, as *H. prosopidis* and *A. calandreae* took less than 24 hours for hatching, at the time of introduction of invader egg, we excluded those cases where the occupant egg did not hatch by then. The number of replicates in each treatment is shown in Table 2. Detailed observations of the larval competition were also made on some replicates.

Results

Competition with 24 hours time lag. In about 70% of the cases the occupant larvae of *D. basalis* and *H. prosopidis* overcame the invader larvae. The proportions were significantly different from 1 : 1 expectation (G-test, $P < 0.001$). In *A. calandreae* the occupant larvae won in 44 cases and the invader larvae in 42 cases. This proportion was not significantly different from 1 : 1 expectation (Table 2 and Fig. 2).

With 24 hours time lag, when the invader hatched, the occupant had already settled on one particular part of the host body utilizing the resource. Still the occupant was as active as a newly hatched larva when disturbed. The invader larva fed on the host for a few minutes, moved actively around the host body and attacked the occupant

Table 2. Results of intraspecific time-lag larval competition. The second egg was transferred on the same host 24, 48, 72, or 96 hours after the first.

| Species | Time-lag between 2 larvae (hours) | No. of replicates | Total no. of wasps emerged | No. of occupant emerged | No. of invader emerged | No. of host emerged | chi square | P |
|----------------------|-----------------------------------|-------------------|----------------------------|-------------------------|------------------------|---------------------|------------|--------|
| <i>D. basalis</i> | 24 | 96 | 86 | 60 | 26 | 4 | 13.44 | <0.001 |
| | 48 | 94 | 94 | 2 | 92 | 0 | 86.17 | <0.001 |
| | 72 | 91 | 91 | 61 | 30 | 0 | 10.56 | <0.001 |
| | 96 | 90 | 80 | 64 | 16 | 3 | 28.8 | <0.001 |
| <i>A. calandras</i> | 24 | 100 | 86 | 44 | 42 | 9 | 0.05 | 0.9 |
| | 48 | 91 | 85 | 2 | 83 | 4 | 77.19 | <0.001 |
| | 72 | 83 | 83 | 79 | 4 | 6 | 67.77 | <0.001 |
| | 96 | 90 | 84 | 84 | 0 | 9 | 84.0 | <0.001 |
| <i>H. prosopidis</i> | 24 | 92 | 90 | 65 | 25 | 4 | 17.78 | <0.001 |
| | 48 | 97 | 88 | 4 | 84 | 1 | 72.7 | <0.001 |
| | 72 | 92 | 90 | 86 | 4 | 0 | 74.71 | <0.001 |
| | 96 | 96 | 90 | 88 | 2 | 1 | 82.18 | <0.001 |

upon encounter. Since both larvae were active and aggressive, either could eliminate the other by biting (mostly in abdomen) each other, though the above results suggest that in *D. basalis* and *H. prosopidis*, the larvae hatched 24 hrs earlier had advantage in biting, probably due to size difference (in both species body length more than doubled during the first 24 hours (unpublished data)).

Competition with 48 hours time lag. In all three wasp species, when the time difference increased to 48 hours, more than 95% of the emerging wasps were from the invader larvae.

With a 48 hour time-lag, when the invader larva hatched, the occupant had already utilized some portion of the host resource for growth. The occupant larva at this stage was less aggressive, hardly moving. The newly hatched invader larva, while moving around the host body, crawled onto the dorsal part of the occupant larva. It was observed that the skin of the occupant larva in 48 hours was fragile, and could easily be punctured. The invader larva embedded its mandibles into the occupant larva upon encounter. The invader larva remained in this position for some hours, which caused the body fluid to leak from the punctured tissue of the occupant larva. In some cases, the bitten larva became shrunken some hours later after the invader larva left. The corpse of occupant was found rotten after some hours later. The winner continued its feeding and developed on the host resource that was still left to be exploited by the invader larva (host weight decreased only 20-30% after 48 hrs' exploitation by the occupant in all species (unpublished data)). The invader larva overcame the occupant a significant proportion of the time ($P < 0.001$ in all species).

Competition with 72 hours time-lag. In all three wasp species, by 72 hours the occupant larvae had exploited nearly all the host body resource and had themselves grown almost to full size (host weight decreased more than 50% by then (unpublished data)). The occupant larva outcompeted the invader in all three species ($P < 0.001$).

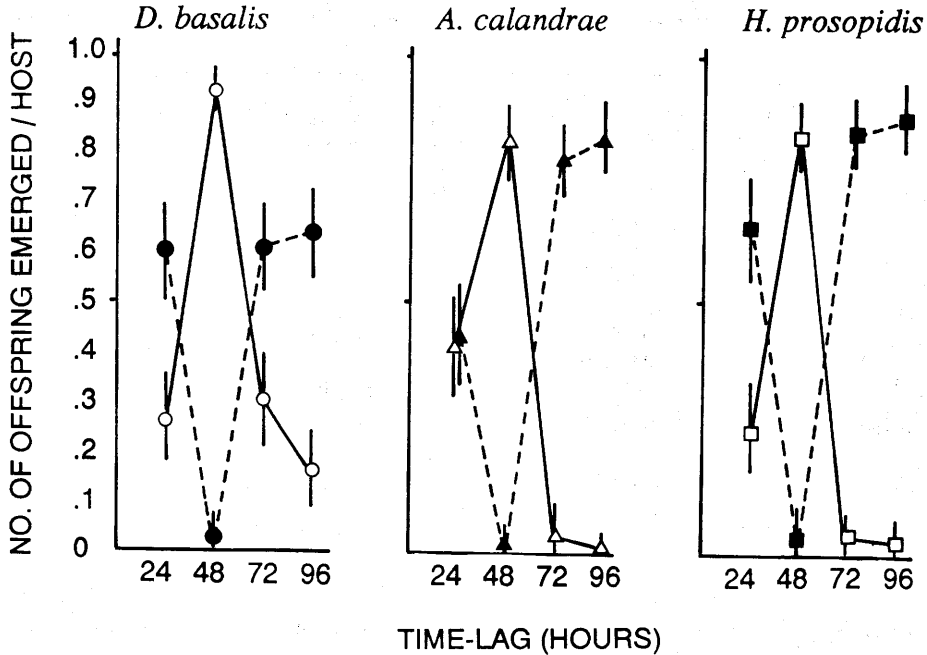


Fig. 2. Mean number of offspring emerged per host in time-lag egg introduction experiment. Solid marks are for occupants, and open marks are for invaders. The vertical bar shows the 95% confidence interval of the mean.

Although most of the invader eggs hatched normally, the invader larvae apparently died of starvation before they began searching for any occupant. In *A. calandreae* and *H. prosopidis*, nearly all adult wasp emerged (more than 95%) were from the occupant larva. In the case of *D. basalis*, however, 30 offspring (33%) were of the invader larvae. When the invader hatched 72 hours after the occupant, the host was almost valueless for the newly hatched larva. Under this condition, some invaders which happened to encounter the occupant larvae nearby cannibalized the well developed occupant larvae and completed development successfully on the occupant larva.

Competition with 96 hours time-lag. With 96 hours time-lag, when the invader larva hatched, the occupant larva had already exploited all the resource and was as large as the host itself. The host body had shrunken and dried by then, and it was totally valueless for the newly hatched invader larva. Most of the invaders died of starvation, and the majority of emerged wasps was of occupant larvae. Still, as with the 72 hours time-lag, 16 invaders of *D. basalis* and 2 invaders of *H. prosopidis* could emerge as adults. They also utilized the occupant as resource by cannibalization.

DISCUSSION

In solitary parasitoids, generally only one offspring emerges from one host. Many studies on the larval competition in a host showed either mutual biting or

physiological suppression operates to remove extra larvae in a host. In most cases, whatever the operating mechanisms are, the older larva usually survives to adult. Thus superparasitism may seem rather disadvantageous, and selected against in nature because of the complete waste of egg(s) for female parent in subsequent oviposition(s). Consequently, many studies have been conducted on the mechanisms to avoid the superparasitism (e.g., Bakker et al., 1967; Ables et al., 1981; Hubbard, et al., 1987). However, most of these works have been done with solitary endoparasitic wasps, and there surprisingly is no work on the larval interaction with solitary ectoparasitic wasps.

In the simultaneous multiple egg transferal experiments with ectoparasitic wasp species, our results showed that regardless of the initial egg density (1, 2, or 5 eggs/host) only one adult emerged from one host in almost all cases. When the adult females produce multiple eggs at one bout, the larvae hatch almost simultaneously, and direct interference competition can occur. Multiple oviposition during a single bout may occur in *A. calandrae* as we often observed 3 or more eggs on one host when we opened the beans to collect parasitoid eggs after short oviposition periods. The present study shows that this 'contest' type competition operates in the earliest larval stage.

In nature, simultaneous oviposition by solitary wasps may be rather unlikely, but sequential ovipositions with some time-lag may take place. In sequential oviposition, our experiments showed that the competitive results depended on the timing of two ovipositions. The first comer is not necessarily the winner, as is often seen in many endoparasitic species. No clear advantage of the occupant over the invader was found in 24 hrs time-lag in *A. calandrae*. However, in *D. basalis* and *H. prosopidis*, the occupant larva had a significant advantage (see Table 2). This probably resulted from the size difference between occupant and invader larvae. Although both were quite active, the occupant had already fed for 24 hours, and was considerably larger than the invader.

In all three wasp species, when the occupant larva was favored by 48 hours, nearly all the invader larvae could overcome the occupant. The competition was of the interference type; the occupant larva was attacked and destroyed by invader. However, there was still enough left of the host resource for the invader to complete its development.

When the occupant larva preceded the invader larva by 72 hours, most of invading *A. calandrae* and *H. prosopidis* larvae died, apparently of starvation. Thus, with a 72 hrs time-lag, exploitative competition was mainly operating. However, in *D. basalis* 30 invaders (33%) successfully emerged as adults. Although the host was mostly consumed when the invader hatched, we saw the occupant larva was often cannibalized by the invader larva. Thus, the larval competition here takes the shape of both 'exploitative' competition and 'interference' competition through 'cannibalism'.

When the occupant larva was given 96 hours' advantage, the larger and older larvae are competitively dominant over younger and smaller larvae. 'Exploitative' com-

petitive mechanism prevailed because the food resource had been totally exploited by the occupant larva. In *D. basalis*, however, 20% of the emerged wasps were of invader eggs, again showing the effect of cannibalism in this species.

The timing and sequence of ovipositions by the wasp females are the main factors determining the outcome of competition among superparasites. These factors control which competitive mechanism operates among larvae, and which larvae (occupant or invader) eventually emerges as an adult after competition.

There are many parasitoid species which complete their life cycle as the endo- or ectoparasites of host insects. They differ in intraspecific competitive mechanisms. Our results show that in the competing solitary ectoparasitic wasp populations, both 'exploitative' and 'interference' competitions are operating. Also, these results show that superparasitism, which often occurs when the hosts are in short supply relative to the wasp density, is not always disadvantageous to the later ovipositor.

Even when the late comers have a competitive advantage due to the difference in interference activity, self superparasitism does not give any adaptive advantage to the female parent. The adaptive advantage occurs only when more than one female lay eggs on a host. In this respect, it is worth noting that the solitary endoparasite, *Nemeritis canescens* (Grav.) tends to avoid superparasitism more on the host in which she herself laid her egg than on host which had eggs laid by others. This may be achieved through the operation of some individual-specific marker, probably originating in Dufour's gland (Hubbard et al., 1987).

Our results show that there is some time window (around 48 hrs time-lag) when a late oviposited egg can be advantageous in intraspecific competition. To utilize this window, however, female wasps must know the precise age of the occupant larva. From the fact that many solitary parasitic wasps rather avoid superparasitism (including *H. prosopidis* and *D. basalis* (unpublished data)), most parasitic wasps may not have this ability, although they have evolved elaborate behavioral mechanism of interference for intraspecific competition.

Some ecologists referred intraspecific competition as the major factor controlling the population dynamics (e.g., Elton, 1947; Nicholson, 1948). The solitary ectoparasitic wasp populations are under 'natural control' through density dependent process caused by intraspecific competition with or without time-lag. We saw that the total number (100) of host larvae could give rise to a similar number of parasitoid offspring (see Fig. 1). Considering the fact that these parasitoid wasps spend most of their life time in the bean (except adult stage), thus having no other major mortality factor such as predation (except disease), the intraspecific larval competition may play the major role in the population dynamics of these species.

SUMMARY

We studied the effect on the intraspecific competitive outcome of time-lags in the

arrival on one host of conspecific eggs of parasitic wasps. We used three species, *Dinarmus basalis*, *Anisopteromalus calandrae*, and *Heterospilus prosopidis*, ectoparasitic on the larvae of azuki bean weevil, *Callosobruchus chinensis*.

We transferred a parasite egg (occupant) onto a host in a clear plastic well, followed by another egg (invader) after a time-lag of 0, 24, 48, 72, or 96 hours. This enabled us to observe directly the competitive process occurring between the wasp larvae on the host.

All three wasp species showed 'contest' type larval competition, in that competition almost always resulted in the emergence of only one wasp offspring from one host regardless of the initial egg density per host and time-lag. However, contrary to many previous studies in which the initial egg laid was usually winner, the competitive outcome depended on the interval of time-lag of two ovipositions.

When the occupant had the 24 hours' advantage, in *D. basalis* and *H. prosopidis*, more than 70% of the emerged offspring were of the occupant larva. Thus in these species, the occupant with 24 hours headstart had a slight (but statistically significant) advantage over the invader. In *A. calandrae*, no significant advantage was observed between two larvae.

When the occupant preceded the invader by 48 hours, in most cases the invader overcame the occupant and emerged as adult. The competition here was strongly of 'interference' type. The resource amount left by occupant was still enough for the invader to complete its development after killing the occupant.

When the occupant was favored by 72 or 96 hours, most of the emerging wasps were of occupant larvae. The occupant had exploited all the resource by then, and the invader apparently died of starvation before attacking the occupant.

Thus the length of the time-lag between two egg introductions determines which egg can survive to adulthood and which competitive mechanism operates. When the ages of the two larvae differed by 24 and 48 hours, the 'interference' competition mechanism (i.e., direct biting) operated. With 72 and 96 hours age differences, the 'exploitation' competition prevailed. In *D. basalis*, however, considerable interference continued even with long time-lag. Thirty three percent of the *D. basalis* invaders with 72 hours time-lag and 18% of the invaders with 96 hours time-lag emerged as adults. This was due to the 'cannibalism'. When the occupant was 72 and 96 hours old, all the host resource had already been used up. However, the invaders developed by feeding on the occupant itself.

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REFERENCES

Ables, J. R., S. B. Vinson, and J. S. Ellis. (1981) Host discrimination by *Chelonus insularis* (Hym.:

- Braconidae), *Telenomus heliothidis* (Hym.: Scelionidae), and *Trichogramma pretiosum* (Hym.: Trichogrammatidae). *Entomophaga* 26(2): 149-156.
- Arora, G. I. and T. Sign (1970) The biology of *Callosobruchus chinensis* (L.) (Bruchidae: Coleoptera). *Res. Bull. Punjab Univ. Sci.*, 21: 55-66.
- Bakker, K., S. N. Bagchee, W. R. van Zwet, and E. Meelis (1967) Host discrimination in *Pseudeucoila bochei* (Hymenoptera: Cynipidae). *Entom. Exp. Appl.* 10: 295-311.
- Bakker, K., J. J. M. van Alphen, F. H. D. van Batenburg, N. van der Hoeven, H. W. Nell, W. T. F. H. van Strien-van Liempt, and T. C. J. Turlings (1985) The function of host discrimination and superparasitization in parasitoids. *Oecologia* 67: 572-576.
- Bellows, T. S., Jr (1979) The modelling of competition and parasitism in laboratory insect populations. Unpublished Ph. D. dissertation, University of London.
- Chow, J. F. and M. Mackauer (1984) Inter- and intraspecific larval competition in *Aphidius smithi* and *Praon pinguicolum* (Hymenoptera: Aphidiidae). *Can. Entomol.* 116: 1097-1107.
- Fisher, R. C. (1961a) A study in insect multiparasitism. I. Host selection and oviposition. *J. Exp. Biol.* 38: 267-275.
- Fisher, R. C. (1961b) A study in insect multiparasitism. II. The mechanism and control of competition for the possession of the host. *J. Exp. Biol.* 38: 605-628.
- Fujii, K. (1983) Resource dependent stability in an experimental laboratory resource-herbivore-carnivore system. *Res. Popul. Ecol., Suppl.* 3: 15-26.
- Hassell, M. P., C. M. Lessells, and G. C. Mcgavin (1985) Inverse density dependent parasitism in a patchy environment: a laboratory system. *Ecol. Entomol.* 10: 393-402.
- Hubbard S. F., G. Marris, A. Reynolds, and G. W. Rowe (1987) Adaptive patterns in the avoidance of superparasitism by solitary parasitic wasps. *J. Anim. Ecol.* 56: 387-401.
- Kariya, H. and M. Kurosawa (1939) Studies on application of a natural enemy to the azuki bean weevil. *Noji-Kairyō-Shiryō* 137: 89-90. (in Japanese)
- Kistler, R. A. (1979) A simple host-parasitoid system: An examination of factors contributing to stability. M. S. thesis, Purdue University.
- Lawrence, P. O. (1988) Intraspecific competition among first instars of the parasitic wasp *Biosteres longicaudatus*. *Oecologia* 74: 607-611.
- Nicholson, A. J (1948) Competition for food amongst *Lucilia cuprina* larvae. *Proc. VII Inter. Con. Entomol., Stockholm*, 227-281.
- Nicholson, A. J (1954) An outline of the dynamics of animal populations. *Austr. J. Zool.* 2: 9-65.
- Okamoto, K. (1971) The synchronization of the life cycles between *Callosobruchus chinensis* (L.) and its parasite *Anisopteromalus calandrae* (Howard). *Jpn. J. Ecol.* 20: 233-237. (In Japanese with English summary).
- Shimada, M and K. Fujii (1985) Niche modification and stability of competitive systems. I. Niche modification process. *Res. Popul. Ecol.* 27: 185-201.
- Utida, S. (1941a) Studies on experimental population of the azuki bean weevil, *Callosobruchus chinensis* (L.). III. The effect of population density upon the mortalities of different stages of life cycle. *Mem. Coll. Agr. Kyoto Univ.* 49: 21-42.
- Utida, S. (1941b) Studies on experimental population of the azuki bean weevil, *Callosobruchus chinensis* (L.). IV. Analysis of density effect with respect to fecundity and fertility of eggs. *Mem. Coll. Agr. Kyoto Univ.* 51: 1-26.
- Utida, S. (1941c) Studies on experimental population of the azuki bean weevil *Callosobruchus chinensis*. V. Trend in population density at the equilibrium position. *Mem. Coll. Agr. Kyoto Univ.* 53: 19-31.

- Utida, S. (1943) Host-parasitoid interaction in the experimental population of the azuki bean weevil, *Callosobruchus chinensis* (L.). III. The effect of host density on the growth of host and parasitoid populations. *Ecol. Rev.* 9: 40-54.
- Utida, S. (1944) Host-parasite interaction in the experimental population of the azuki bean weevil, *Callosobruchus chinensis* (L.). II. The effect of density of parasite population on the growth of the host population and also of the parasite population II. *Oyodobutsu* 15: 2-18.
- Utida, S. (1948) Host-parasite interactions in the experimental population of the azuki bean weevil, *Callosobruchus chinensis* (L.). IV. *Oyo-Kontyu* 4: 164-174. (In Japanese).
- Utida, S. (1953) Population fluctuation in the system of host-parasite interaction. *Res. Popul. Ecol.* 2: 22-46 (in Japanese with English summary).
- Utida, S. (1955) Population fluctuation in the system of interaction between a host and its two species parasite. *Oyo-Kontyu* 11: 43-48 (in Japanese with English summary)
- Utida, S. (1957) Population fluctuation, an experimental and theoretical approach. *Cold Spring Harbor Sympo. Quant. Biol.* 22: 139-151.
- Van Dijken, M. and J. K. Waage (1990) Self and conspecific superparasitism in *Trichogramma evanescens* Westwood. *Entomol. Exper. Appli.* (in press)

マメゾウムシ幼虫の外寄生蜂の間で見られる幼虫期種内競争

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複数の同種寄生蜂卵が時間差を持って寄主に産卵された時、時間差が種内競争の結果に及ぼす影響について実験的に研究した。実験材料としてマメゾウムシ幼虫に外寄生する3種の寄生蜂、*Dinarmus basalis*, *Anisopteromalus calandrae*, *Heterospilus prosopidis*, を用いた。

アクリル製の板に作った穴に入れた寄主の上に、まず第一（先住者）の寄生蜂卵を導入し、0, 24, 48, 72, または96時間後に第2（侵入者）の寄生蜂卵を導入した。これによって、寄主上での寄生蜂幼虫間に起こる種内競争の過程を直接観察することが可能になった。

3種はいずれも“コンテスト”型の競争を示し、寄主当たりの寄生蜂卵密度や卵導入の時間差にかかわらず、常に1匹の寄生蜂成虫が羽化した。しかし、先住者が常に種内競争に有利であるというこれまでの多くの研究結果とは異なり、競争結果は2個の卵の寄主上への到着時間の時間差に依存した。

先住者が24時間先に寄主上に導入された時には、*D. basalis* と *H. prosopidis* では、羽化した寄生蜂の70%以上は先住者であった。これら2種では、24時間の時間差を持った先住者は侵入者に対して統計的に有意に競争に強かった。しかし *A. calandrae* では2者の間に優劣関係は見られなかった。

2者の導入の時間差が48時間の時には、ほとんどの場合、侵入者が先住者を噛み殺し、成虫として羽化した。この場合の競争形態は明らかな“干渉型”であった。先住者が使い残した資源量は、侵入者が先住者を噛み殺した後、成虫まで発育するのに十分であった。

2者の時間差が72, または96時間になった時には、羽化寄生蜂の大部分は先住者であった。これらの時間差では、侵入者が寄主上に導入された時には資源はすでに先住者によってほとんど利用しつくされており、侵入者は先住者を攻撃する前に餓死したと思われる。

以上の結果から、2個の卵が時間差をもって産卵された時に、どちらの卵が成虫になれるか、またどのような競争様式が競争結果を決めるのかには、2個の卵が寄主上に到着する時間差が決定的な役割をはたしていることが明らかになった。24, または48時間の時間差では干渉型（噛合い）競争が起こり、72, または96時間の時間差では消費型競争が競争結果を決めた。しかし *D. basalis* では、長時間の時間差でも干渉型競争（“共食い”）が見られた。羽化成虫のうち、72時間の時間差では33%が、96時間でも18%が侵入者であった。72, または96時間の時間差では、寄主（資源）はすでに先住者によって利用しつくされており、侵入者は先住者を餌として発育をし、羽化した。