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Host Discrimination and Factors Affecting Incidence of Superparasitism in *Hemiptarsenus varicornis* (Hymenoptera: Eulophidae), a Parasitoid of the Leafminer *Liriomyza trifolii* (Diptera: Agromyzidae)

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An ovipositing parasitoid can save searching time, energy and eggs by avoiding superparasitism, and superparasitism avoidance hence is a factor that affects searching efficiency of a parasitoid. This study examined host discrimination and environmental factors causing superparasitism in the solitary parasitoid wasp *Hemiptarsenus varicornis*, a promising candidate for biological control of dipteran leafminers such as *Liriomyza trifolii* and *L. sativae*. Cage experiments showed that the pattern of parasitoid egg distributions among hosts skewed significantly from the Poisson distribution. This suggested that *H. varicornis* had the host-discrimination ability. However, superparasitism avoidance was not perfect; hosts that had received two parasitoid eggs were observed. Accordingly, factors affecting the incidence of superparasitism were examined. Superparasitism was observed only for third host larval instars, the most suitable host stage for parasitoid development. Superparasitism occurred more frequently when females laid more eggs, suggesting that females with a greater motivation to oviposit were more likely to superparasitize. The level of superparasitism also increased when fewer numbers of third host instars were available for females. The number of second instars of *L. trifolii* available did not affect superparasitism incidence on third host instars. Host discrimination and superparasitism in *H. varicornis* are discussed in terms of its searching efficiency and mass-rearing procedure.

INTRODUCTION

Leafminer insects such as *Liriomyza trifolii* (Burgess) and *L. sativae* Blanchard (Diptera: Agromyzidae) cause serious damage to many agricultural crops (e.g., Levins *et al.*, 1975; Schuster *et al.*, 1976; Minkenberg and van Lenteren, 1986; Parrella, 1987; Spencer, 1989; Rauf *et al.*, 2000; Tran *et al.*, 2007a). Because they have developed insecticide resistance (e.g., Parrella *et al.*, 1984; Mason *et al.*, 1989; Saito *et al.*, 1992; Ohno *et al.*, 1999a, b), dipteran leafminers are often difficult to control exclusively with chemicals. Therefore, research has been conducted to test various IPM strategies and combinations of different control methods against pest leafminers (e.g., Trumble, 1985; Minkenberg and van Lenteren, 1986, 1987; Heinz and Parella, 1993; Weintraub and Horowitz, 1998; Ohno *et al.*, 1999a; Ozawa *et al.*, 1999, 2001; Weintraub, 2001).

Parasitoid wasps are shown to suppress dipteran leafminers in greenhouses throughout Europe, Japan and North America; two commercialized parasitoid species, *Diglyphus isaea* (Walker) (Eulophidae) and *Dacnusa sibirica* Telenga (Braconidae), are commonly used as control agents (Wardlow, 1985; Minkenberg and van Lenteren, 1986, 1987; Saito *et al.*, 1995; Ozawa *et al.*, 1999, 2001). Also, in North America, the eulophid parasitoid *Diglyphus begini* (Ashmead) can successfully control *L. trifolii* (Heinz and Parella, 1990; Heinz *et al.*, 1993).

More recently, *Hemiptarsenus varicornis* (Girault)

has discovered as a major parasitoid of *L. trifolii* in Japan (Saito *et al.*, 1996, 1997; Arakaki and Kinjo, 1998; Ozawa *et al.*, 2001; Ohno *et al.*, 1999b). *H. varicornis* is in the Eulophidae family and is native to Japan, Indonesia, and probably to other part of East and South-East Asia (Konishi, 1999). This parasitoid increases its population in greenhouses and can become predominant over *D. isaea* and *D. sibirica*, which have been released to control *L. trifolii* (Ozawa *et al.*, 2001). Parasitism of *L. trifolii* by *H. varicornis* is also high in subtropical regions (Arakaki and Kinjo, 1998; Rauf *et al.*, 2000). Thus, the parasitoid is a promising agent for controlling pest leafminers.

H. varicornis flies or hops from leaf to leaf where host leafminers can be present. On the leaf, the parasitoid walks and drums the leaf with its antennae to search and feel for leafminer larva on the leaf. Once it encounters a mine in the leaf, it starts to search along with the mine, mostly in the direction to which the target host larva is present (Ayabe and Ueno, 2004). The adult wasps that emerge feed on leafminer larvae for host feeding (Ho and Ueno, 2002, 2007). *H. varicornis* develops mainly in the second and third instars of the leafminers (Bordat *et al.*, 1995).

Relatively few studies have investigated the life history and biology of *H. varicornis*. Many biological parameters that are required to assess as a biocontrol agent still have poorly been known. Host discrimination and superparasitism are among such biological characteristics. Accordingly, the present study focuses on host discrimination and superparasitism in *H. varicornis*.

Superparasitism refers to parasitization of an indi-

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vidual host by more larvae of a single parasitoid species than can mature on that host individual (van Alphen and Visser, 1990; Godfray, 1994; Ueno, 1997, 1999a; Dorn and Beckage, 2007). For solitary parasitoids, in which only one parasitoid can develop to an adulthood on a single host individual, superparasitism takes place when more than one egg are laid on a single host individual. A single female individual or a succession of females of the same species may lay eggs on a host that has been previously parasitized. Superparasitism results in a waste of eggs through lethal competition among parasitoid larvae (e.g., Harvey *et al.*, 1993; Godfray, 1994; Ueno, 1997; Dorn and Beckage, 2007). In some cases, superparasitism causes direct mortality of hosts, leading also to a waste of parasitoid progeny (Ueno, 1997). Thus, the production efficiency of parasitoids for biological control should decrease when superparasitism occurs frequently in laboratory rearing systems. To produce biological control agents efficiently, we need the knowledge of laboratory environments in which the incidence of superparasitism can be minimized.

Avoidance of superparasitism is also important for parasitoids to be an efficient forager. Superparasitism avoidance is attained by avoiding parasitized hosts directly or by avoiding areas where parasitized hosts are present. Host discrimination, an ability of an ovipositing parasitoid to discriminate between parasitized and unparasitized hosts, is a general mechanism by which parasitoids avoid superparasitism (van Lenteren, 1981; Hofsvang, 1990; Godfray, 1994). Therefore, investigation of host discrimination and superparasitism avoidance in a parasitoid will help uncover to assess whether it can be an efficient forager, or a potentially effective biocontrol agent.

The purpose of the present study is to evaluate the host discrimination ability in *H. varicornis* and to examine factors influencing superparasitism avoidance in this parasitoid. Knowing factors that deter superparasitism avoidance in *H. varicornis* will help assess environmental conditions in which the parasitization efficiency can be disruptive. This information will help improve mass-rearing systems of *H. varicornis*.

MATERIALS AND METHODS

Parasitoids and hosts

Culture of host leafminer *Liriomyza trifolii* was maintained using kidney bean plants. The parasitoid *Hemiptarsenus varicornis* were reared on larvae of the leafminer. General methods for rearing *L. trifolii* and *H. varicornis* are described by Ho and Ueno (2002, 2007).

Cage experiment

Kidney bean plants infested with large numbers of 2nd and 3rd instars of *L. trifolii* were used in this experiment. Potted plants with leafminers were individually placed in a transparent plastic box (20 cm*20 cm*35 cm) and then one female *H. varicornis* was carefully introduced into the box. Tissue paper saturated with diluted honey (20%) was also placed in the box to provide

female parasitoids with food.

Female *H. varicornis* were allowed to attack leafminers for 24 hours. After a 24h exposure, plants were removed from the cage, and leafminers within leaf tissues were checked under a binocular stereoscopic microscope. For each leafminer, the larval instar (2nd or 3rd instars) was noted and the number of parasitoid eggs on the leafminer was recorded. When a single leafminer larva received more than two parasitoid eggs, then it was regarded that superparasitism took place on that larva.

This treatment was repeated for 5 consecutive days for each female parasitoid; thus a total of 5 plants with leafminers were given (female age: 1–5 days). The experiment was conducted at 25 ± 1 °C under a constant light. In all, 14 females of *H. varicornis* were used in the experiment.

Data analyses

Statistical treatments were made with the aid of JMP (SAS Institute, 2001). Because many test females attacked few hosts in the first and second days of the experimental period, data taken between the third and fifth days (female age: 3–5 days old) were used in the following analyses. Superparasitism avoidance was examined using chi-squared test, with which comparison was made between parasitoid egg distributions among hosts and expected distributions in case no discrimination took place. Expected egg distributions were calculated on the basis of the Poisson distribution, in which it was assumed that (1) parasitoids encountered hosts at random; (2) parasitoids might lay one egg or might avoid superparasitism upon encountering with a parasitized host; and (3) the probability of avoidance was independent of the number of parasitoid eggs already present on the host. Data obtained during the experiment for 3 days were pooled for each test female parasitoid, and the analysis was made for each female parasitoid.

Factors causing superparasitism were then examined. Stepwise methods were first used to pick up significant parameters, and a multiple regression model was then obtained. Leverage plots were used to show the relationships between incidence of superparasitism and a given factor being significant. The percentages of superparasitism incidence calculated for each test female were used as a dependent variable and were subject to the analyses after arcsine square root transformation. Three factors, i.e., the numbers of 2nd and 3rd host instars given for each female and the total number of eggs laid by the female, were evaluated as independent variables. Non transformed data were reported.

RESULTS

Superparasitism by *H. varicornis* was observed in our laboratory test though the level of superparasitism was generally very low. Because female *H. varicornis* strongly preferred 3rd over 2nd host instars of *L. trifolii* for oviposition and because no superparasitism was observed for the 2nd larval instars, data were analyzed only for 3rd instars. The percentages of superparasitism

incidence (superparasitized 3rd host instars/parasitized host 3rd instars*100) varied among test females, ranging from 0% to 40.0% (Table 1). The mean percentage of hosts (with ± SE) that had received multiple parasitoid eggs was 7.38 ± 2.66%.

The presence of host discrimination was evaluated by examining patterns of egg distributions. Egg distributions were significantly different from Poisson distributions for data from 7 out of 14 test females (Table 1). Overall, the number of hosts receiving multiple eggs (=superparasitized hosts) was much fewer than that expected from random egg distributions. In fact, the numbers of superparasitized hosts observed were fewer than the expected numbers of superparasitized hosts from Poisson distributions (Fig. 1). The results of our experiments strongly suggested that *H. varicornis* had the host-discrimination ability.

The relationships among three independent variables, i.e., the numbers of 2nd and 3rd host instars given for

each female and the total number of eggs laid by the female, were examined. No significant correlations were detected. Stepwise regression analysis was then made to select factors affecting the levels of superparasitism. The number of 2nd instars given to each test female was not significant and was excluded from the following model. A multiple regression analysis was made with the remaining two factors to determine the relationships between the two and superparasitism. The model obtained was significant ($r^2=0.542$, $N=14$, $F=6.499$, $P=0.014$), and the number of host 3rd instars given and the number of eggs laid were both found significant (Table 2). The interaction between the two factors was not significant and was not included in the model. Leverage plots showed a negative relationship between superparasitism and the number of 3rd host instars given (Fig. 2a) while a positive relationship was detected

Table 1. Incidence of superparasitism in *Hemiptarsenus varicornis*

Wasp no.	Total hosts	% superparasitism	χ^2 values*	P values
1	106	17.65	2.98	0.084
2	83	0	6.90	0.009**
3	59	40.0	0.36	0.55
4	123	7.69	0.13	0.71
5	180	0	2.48	0.12
6	184	0	6.63	0.010**
7	141	5.41	4.44	0.035**
8	225	2.78	5.99	0.014**
9	106	4.76	0.40	0.53
10	176	3.45	2.39	0.12
11	58	0	3.84	0.049**
12	144	3.23	3.46	0.063
13	116	12.82	5.62	0.018**
14	266	0	9.38	0.002**

* Chi-squared values represent divergence from the Poisson distribution.

** P values that are significant.

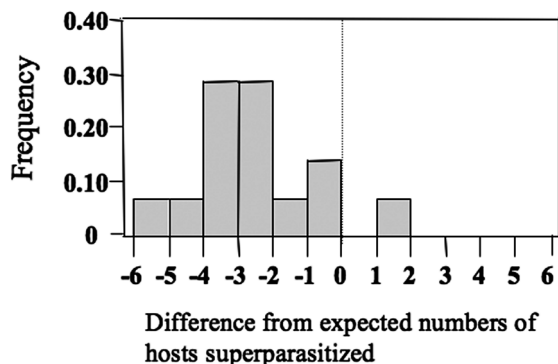


Fig. 1. The remainders of subtracting the expected from the actual numbers of superparasitized hosts. The majority of the values are below zero, suggesting the tendency of female *H. varicornis* avoiding superparasitism.

Table 2. The result of multiple regression analysis for factors affecting the level of superparasitism

Factors	t values	P values
# eggs laid	2.22	0.053
# 3 rd instars	-2.80	0.005

Whole model: $r^2=0.542$, $N=14$, $F=6.499$, $P=0.014$.

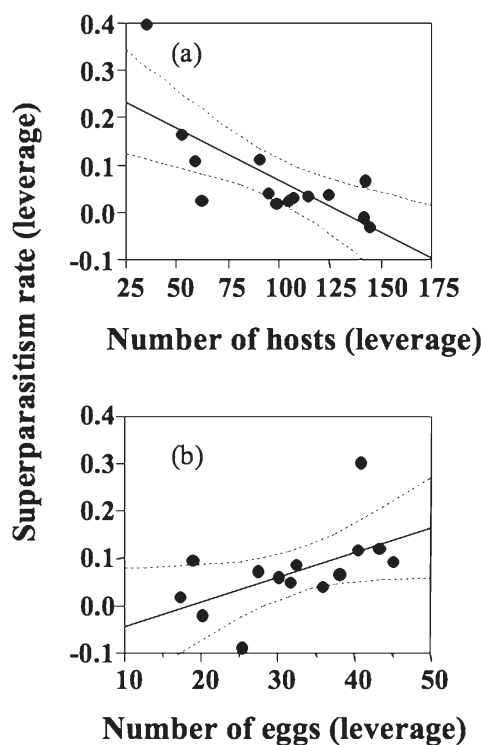


Fig. 2. Leverage plots for testing whether the two factors included in the multiple regression model (see Table 2.) significantly correlate to the rate of superparasitism observed. (a) The relationship with the total number of eggs laid by female parasitoids and (b) that of hosts given to them during a 3 day experimental period. Dotted lines show 95% confidence curves. Statistical results are given in Table 2.

between superparasitism and the number of eggs laid during the experiment (Fig. 2b). Thus, when suitable hosts, 3rd larval instars of *L. trifolii*, were few, female *H. varicornis* commit superparasitism. Also, females that carried and laid more eggs were more likely to superparasitize.

DISCUSSION

Superparasitism Avoidance

An indigenous larval parasitoid, *H. varicornis*, appears to be effective in controlling dipteran leafminers (Ozawa *et al.*, 2001). Part of the reasons would be that *H. varicornis* is an efficient forager. Having a high ability of avoiding superparasitism may be a behavioral mechanism of being an efficient forager because superparasitism avoidance allows a foraging female to save time, energy and eggs (van Alphen and Visser, 1990; Weisser and Houston, 1993). Thus, the presence of a strong tendency to avoid superparasitism may partly explain why *H. varicornis* is an effective parasitoid.

The present paper demonstrates that *H. varicornis* is capable of avoiding superparasitism. The mechanisms by which *H. varicornis* avoids superparasitism are not known. Many literatures have given evidence that an ovipositing parasitoid deposits chemical markers on or in a host (host-marking pheromones), which allows it or females subsequently encounter that host to recognize prior parasitism (van Lenteren, 1981; Hofsvang, 1990; Godfray, 1994). Female parasitoids can thereby discriminate between parasitized and unparasitized hosts. The presence of such marking pheromones is not examined for *H. varicornis*. However, some parasitoids attacking dipteran leafminers do use marking pheromones to avoid a previously parasitized host and/or a previously searched area (Sugimoto *et al.*, 1986). It is likely that *H. varicornis* uses a similar system. Future research will uncover this point.

Factors causing superparasitism

Although *H. varicornis* had the host discrimination ability, discrimination was not always perfect; superparasitism did occur in the present study. For many parasitoids, superparasitism has frequently been observed in the laboratory (van Lenteren, 1981; van Alphen and Visser, 1990; Ueno, 1999a). There are a number of explanations why superparasitism does take place (van Alphen and Visser, 1990; Weisser and Houston, 1993). A major factor is host density; when there are a limited number of hosts, female parasitoids begin to commit superparasitism (van Lenteren, 1981). This was the case for *H. varicornis*. When 3rd instars of leafminers were fewer, the number of hosts that were superparasitized increased significantly. However, the number of second host instars did not influence the incidence of superparasitism. In our experimental set-up, *H. varicornis* parasitized mostly on 3rd instars, and this is because they are most suitable for development of larval *H. varicornis*. Difference in host quality between 2nd and 3rd instars may explain why the number of less suitable, sec-

ond instars do not affect superparasitism incidence.

Theory predicts that another factor causing superparasitism may be the level of females' motivation to oviposit (Fletcher *et al.*, 1994; Ueno, 1999b). For example, female parasitoids with a greater number of mature eggs are more likely to accept low quality hosts including parasitized hosts (Fletcher *et al.*, 1994). If this could be the case, the incidence of superparasitism would be greater for females that lay more eggs within a given period of time. To test this, the relationship between the number of eggs laid and the level of superparasitism was examined in our study. The results demonstrated a positive relationship between the two, supporting the idea that females with a greater oviposition potential are more likely to superparasitize.

Mass-rearing of parasitoids

Use of native parasitoids is an important approach in IPM of *Liriomyza* spp. in Japan and Vietnam (Ueno, 2006; Tran *et al.*, 2007b). If native parasitoids are to mass-rear for release, then effective procedures of mass-rearing are required. Our study suggests that female *H. varicornis* can commit superparasitism in laboratory mass-rearing systems, particularly when ovipositional pressures are great and suitable 3rd instars of hosts are scarce. When superparasitism occurs frequently, many parasitoid eggs should die before maturity because of lethal combat among parasitoid larvae hatched (van Lenteren, 1981). In addition, the quality of parasitized hosts can be lowered because of an increased parasitoid load, causing the production of low-quality parasitoids in terms of the size. The proportion of parasitized hosts that yield the offspring parasitoid can also decrease due to repeated attack of hosts (Harvey *et al.*, 1993; Ueno, 1997; Dorn and Beckage, 2007).

Thus, the efficiency of parasitoid mass-rearing should be decreased if superparasitism could frequently take place. It is desirable to use rearing conditions in which the incidence of superparasitism is kept at minimum. The provision of sufficient numbers of suitable hosts, i.e., 3rd instars of *L. trifolii*, is favorable in terms of reducing superparasitism. Basing on the data obtained in the present study, we suggest that at least around 30–40 leafminers of the 3rd larval instars should be secured per female parasitoid together with 2nd instars for host feeding when hosts are provided for females at a daily basis.

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