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Improving Parasitoid Performance by Improving Adult Food Quality: A Case Study for the Leafminer Parasitoid *Hemiptarsenus varicornis* (Hymenoptera: Eulophidae)

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Leaf miners of the family Agromizyidae contain many pest species that are often difficult to control exclusively with insecticides due to high levels of resistance. Biological control with insect parasitoids is an alternative or compatible option in leafminer management. Effective mass rearing systems of parasitoids are essential to successful biocontrol because cost of parasitoid production is often too high and lowering the cost is crucial to economically reasonable practices of biological control. Experiments were conducted to examine whether provision of protein sources as supplemental food could improve mass rearing efficiency of *Hemiptarsenus varicornis*, a parasitoid wasp attacking the leafminer *Liriomyza trifolii*. No significant difference was found in the number of ovipositions and host-feedings between female groups, i.e., females that had been fed on a honey solution and those fed on a honey–protein mixture. Females that fed on more hosts parasitized more hosts, suggesting that host-feeding was involved in an enhancement of egg production in *H. varicornis*. However, the relationships between the number of host-feedings and ovipositions did not differ between the female groups. These results indicated that provision of skim milk as a protein source did not improve parasitoid production. We discuss the importance of nutritional ecology and physiology of parasitoids for the fundamental understanding of parasitoid reproduction.

INTRODUCTION

Leaf miners belonging to the family Agromizyidae (Diptera) include serious pests of numerous vegetable crops such as beans, cucumber, potato and crucifers in the world (e.g. Parrella *et al.*, 1984; Wardlow, 1985; Minkenberg and van Lentren, 1986; Parrella, 1987; Sheng *et al.*, 1989; Thang, 1999; Rauf *et al.*, 2000; Tran *et al.*, 2006; Ueno, 2006). Yield loss due to dipteran leaf miners can be considerable when the management is unsuccessful (Parrella *et al.*, 1984; Parrella, 1987; Spencer, 1989). In Asian countries including Vietnam and Japan, *Liriomyza trifolii* is among such important pest leaf miners (e.g. Sivapragasam *et al.*, 1999; Ohno *et al.*, 1999a, b; Thang, 1999; Tran *et al.*, 2006).

Liriomyza trifolii has developed pesticide resistance, and control of this pest exclusively with pesticides is difficult (e.g. Parrella *et al.*, 1984; Wardlow, 1985; Weintraub and Horowitz, 1998; Ohno *et al.*, 1999a, b; Weintraub, 2001). Biological control with natural enemies (parasitoids and predators) can provide good control against such insect pests (Greathead, 1986; Waterhouse and Norris, 1987; Parrella, 1987). In fact, parasitoid wasps have recently proven successful as an agent of biological control of leafminers (e.g. Minkenberg and van Lenteren, 1986; Parrella *et al.*, 1987; Ozawa *et al.*, 1998, 1999, 2001; Weintraub, 2001).

Although many parasitoids were recorded from *L. trifolii*, most recent studies have suggested that *Hemiptarsenus varicornis*, a solitary larval ectopara-

sitoid, is a promising agent at least in Japan (Saito *et al.*, 1995; Arakaki and Kinjyo, 1998; Konishi, 1988; Ohno *et al.*, 1999a, b; Ozawa *et al.*, 1999, 2001). However, relatively few studies have examined the biology and life history of this parasitoid (Bordat *et al.*, 1995; Saito *et al.*, 1995; Ho and Ueno, 2002), and basic information available for this parasitoid is still limited.

Biological characteristics that are essential to evaluating the potential of a certain parasitoid species as a biocontrol agent include: development time, adult longevity, fecundity, host range, host-finding capacity, host selection behavior etc. In the former paper, we have investigated development time, adult longevity and fecundity of *H. varicornis* (Ho and Ueno, 2002). Here, we focus on the effect of nutrition on oviposition activity of *H. varicornis* in the laboratory.

Adult food is an important determinant of fecundity of female parasitoids (Jervis and Kidd, 1986, 1996; Godfray, 1994; Ueno, 1999; Heimpel and Jervis, 2005). By feeding on host blood, female parasitoids including *H. varicornis* can gain nutrients for egg production (Jervis and Kidd, 1986; Heimpel and Collier, 1996; Morales-Ramos *et al.*, 1996; Ueno, 1999; Ueno and Ueno, 2004). In addition, many species of parasitoids feed on floral nectar, aphid honeydew etc, which can be food sources for maturing eggs (e.g. Jervis *et al.*, 1993; Jervis and Kidd, 1996; Idris and Grafius, 1997; Rojas *et al.*, 1998; Schmale *et al.*, 2001; Heimpel and Jervis, 2005). The presence and availability of adult food can determine the success of biological control with parasitoids (van Emden, 1990; Jervis *et al.*, 1996; England and Evans, 1997; Heimpel and Jervis, 2005; Lavandero *et al.*, 2005). Further, supplemented adult diet during mass-rearing process may improve the efficiency of parasitoid production, resulting in a reduction of the

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production cost.

We therefore expect that a close relationship between oviposition and host or non-host meal should occur in the parasitoid *H. varicornis*. Also, we expect supplemented adult food should enhance oviposition activity of *H. varicornis*. In the present study, we evaluate the relationship between host feeding and oviposition activity and also the effect of provision of a protein source for female parasitoids on the activity. Based on the results, the importance of adult food for *H. varicornis* reproduction is discussed.

MATERIALS AND METHODS

General Rearing Procedure

Seeds of kidney bean were planted in plastic pots (7.5 cm in diameter). After one week of germination, a pan (32 cm*44 cm*6 cm) containing 24 potted kidney bean plants was placed on a large shelf covered with a fine meshed nylon. Leafminer adults were released into the shelf for oviposition. After a 24 h exposure for oviposition, the potted plants were removed from the shelf and were maintained at $25 \pm 1^\circ\text{C}$ until all leafminer larvae were matured. Leaves with mature larvae were cut off from the plants, and were placed in the shelf for adult leafminer emergence, together with new potted host plants.

Hemiptarsenus varicornis was reared on larvae of *L. trifolii*. Kidney bean plants infested with large numbers of 2nd and 3rd instars of *L. trifolii* were introduced into a transparent plastic box (20 cm*20 cm*35 cm), one side of which was covered with a fine meshed nylon. Female parasitoids were then introduced into the box. Tissue paper saturated with a 30% honey solution was also placed in the box as a food source for female parasitoids. Female parasitoids were allowed to attack and parasitized leafminer larvae for 24 hours. After 24 hours for parasitism, plants with parasitized hosts were removed from the box, and were kept in the rearing room ($25 \pm 1^\circ\text{C}$, 24L) for 5–7 days. Leaves containing parasitized larvae were then cut off from the plants, and were placed in a rearing plastic box (19 cm*25 cm*9 cm) for parasitoid emergence.

Experimental procedures

As a non-host meal, we provided females with 20% skim milk plus honey solution to examine the effect of provision of protein source on female reproduction. Kidney bean plants infested with large number of 2nd and 3rd instars of *L. trifolii* (around 40–60 host larvae) were used in this experiment. Plants with leafminers were individually placed in a transparent plastic box (see the General rearing procedure) and then one female *H. varicornis* was carefully introduced into the box. Tissue paper saturated with a 20% honey solution or a 20% skim milk and honey solution was also placed in the box in order to provide female wasps with food. Females provided with honey solution are assigned as control group, and those with skim milk plus honey solution as additional protein group. As a pre-experimental

treatment, both groups of *H. varicornis* were allowed to attack leafminer larvae for 24 hours from day 1 to day 3 after wasp emergence.

On day 4, a host plant with leafminer larvae was placed in a box where one test female was kept. After a 24h exposure, plants were removed from the box, and leafminers within leaf tissues were checked under a binocular microscope. The number of parasitoid eggs and leafminer age (2nd or 3rd instars) were recorded. Care was taken to examine whether hemolymph of host leafminers was exuded on the body surface or not. When host hemolymph was exuded on a host larva, we regarded that the host was fed on.

This procedure was repeated for 2 consecutive days; thus a total of 2 plants with leafminers were given to each female wasp (female age: 4–5 days). The experiment was conducted at $25 \pm 1^\circ\text{C}$ under constant light. In all, 24 female wasps were used. The data were summed for each test wasp and were analyzed with the aid of JMP version 3.2 (JMP, 1997). Variance and normality of the data were first checked, and then parametric statistical treatments were made. An ANCOVA was performed to assess the effect of food type and host feeding on the number of hosts parasitized. Simple regression analyses were made to examine the relationships between the numbers of hosts fed upon and those parasitized. The mean number of hosts parasitized was compared between the female groups with an ANOVA.

RESULTS AND DISCUSSION

Each female oviposited around 24 host instars and used 6–8 hosts for feeding purposes (Fig. 1). No host individuals were used for both oviposition and feeding purposes. The mean number of hosts parasitized did not differ between the female groups (Fig. 1a; ANOVA, $F = 0.001$, $P = 0.97$). Also, the mean number of hosts that had been fed upon did not differ depending on food types (Fig. 1b; ANOVA, $F = 1.89$, $P = 0.18$). The total numbers of leafminers killed during the 2-day-experimental period were not significantly different (Fig. 1c; ANOVA, $F = 0.08$, $P = 0.78$). These results demonstrated that provision of skim milk as a protein source did not affect the reproduction of female *H. varicornis*. We would expect an enhancement of female reproduction by adding a protein source to adult food; contrary to this expectation, reproductive improvement was not detected, at least, in our experimental set up with *H. varicornis*.

H. varicornis killed considerable numbers of hosts via host-feeding (Fig. 1b). Because the number of hosts parasitized and those fed upon considerably varied among test parasitoid individuals, an ANCOVA was performed in order to assess the effects of food type and host feeding on the number of hosts oviposited. The whole model obtained was highly significant (Table 1; $P = 0.0001$). The analysis showed that host feeding, i.e. the number of hosts that had been used for feeding purpose, was the sole factor affecting *H. varicornis*

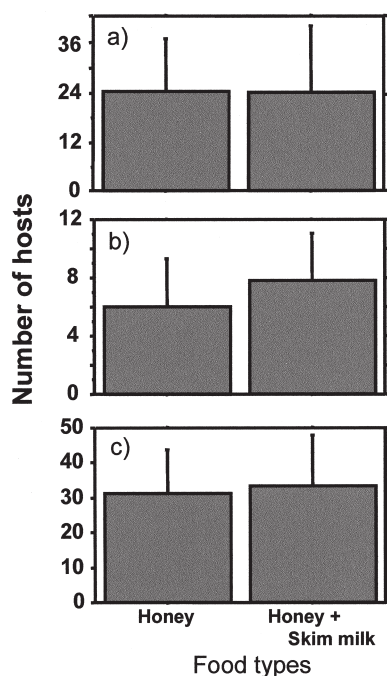


Fig. 1. Effects of food types that were given for female *Hemiptarsenus varicornis* on the number of hosts parasitized (= oviposited) (1a), hosts fed upon (1b), and the total number of hosts killed via parasitism and host-feeding (1c). Bars and lines above the bars indicate the means and SD, respectively. No significant differences were detected between the groups (ANOVA, $P > 0.05$).

oviposition, i.e. the number of hosts parasitized (Table 1). Food type and interaction term were not significant. Again, the food effect was not detected even when individual differences in the number of hosts fed on among test females were taken into consideration.

Significantly positive relationships were detected between total numbers of hosts fed upon and those parasitized (Fig. 2) (Regression analyses: $r^2 = 0.63$, $t = 4.15$, $P = 0.002$ for the control; $r^2 = 0.49$, $t = 3.10$, $P = 0.011$ for the skim milk treatment group). These results suggest that females that feed more can parasitize more. Host-feeding is an essential means of obtaining proteins for a number of parasitoid species, and feeding activities correlate to female fecundity (e.g. van Lenteren *et al.*, 1987; Heimpel and Collier, 1996; Jervis and Kidd, 1996; Jervis *et al.*, 1996; Morales-Ramos *et al.*, 1996; Ueno, 1999). This appears to be the case for *H. varicornis*. The results also suggest that 50–60% variations in the number of hosts parasitized by each test female can be explained by differences in the number of hosts fed on.

Table 1. The result of ANCOVA* for the numbers of hosts parasitized by *Hemiptarsenus varicornis* during a 48-hours-experimental period

Factors	Sum of Squares	F-value	P-value
Food types	11.7	0.59	0.45
# of hosts fed on	435.9	22.2	0.0001
Interaction	0.9	0.04	0.84

* Whole model obtained was highly significant ($P < 0.0001$).

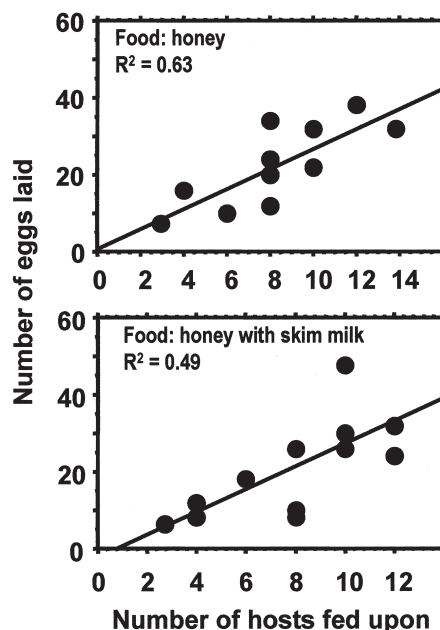


Fig. 2. Relationships between the number of hosts that female *Hemiptarsenus varicornis* fed on and the number of hosts parasitized. For both food type groups, significantly positive relationships were detected (regression analyses, $P < 0.01$), suggesting a close relationship between egg production and host-feeding.

However, why variation in the number of hosts fed upon occurs remains unsolved.

H. varicornis is synovigenic and newly emerged females carry no or only a few mature eggs. Egg production begins after adult emergence from the host and the number of mature eggs in the ovary rapidly increases when hosts are available (Ho and Ueno, 2002). We used 4–5 days old females in which the level of oviposition activity is high. However, female *H. varicornis* can live around 2 weeks, and hence 4–5 days old females would continue egg production at least for one week. We failed to detect food effects in the present study. The failure may be because 3-day-pre-experimental period is not enough to detect the enhancement of egg production through an additional protein source.

Alternatively, proteins in skim milk may not be digested or cannot be used by adult *H. varicornis* though skim milk has been shown as a suitable source of protein in order to prepare artificial diets for rearing immature parasitoids (e.g. Morales-Ramos *et al.*, 1996; Thompson, 1999). In fact, in some parasitoids, egg production is differently influenced via host feeding depending on host species, suggesting that the difference in amino acids or proteins influences differently female reproduction of parasitoids (Leius, 1962; Rojas *et al.*, 1998). It is therefore important to choose materials to be added in parasitoid food. The understanding of nutritional physiology in parasitoid reproduction is then crucial to improving adult food to be given in the laboratory. However, nutritional physiology of parasitoids is rather an overlooked area, and future studies should address this subject.

Females of most synovigenic parasitoid wasps that feed on host hemolymph (blood) have to make choice to feed, or to oviposit, upon hosts because hosts that are fed upon are not suitable for offspring development (Heimpel and Collier, 1996; Ueno, 1999, 2000). Because hosts that are fed upon are not used for oviposition and because female parasitoids may feed on a considerable proportion of hosts given in the laboratory, mass-rearing efficiency cannot be maximized if females should use many hosts presented in the rearing system. Provision of additional protein food is thus ideal to reduce the proportion of hosts used for feeding purposes.

Host-feeding is known for eulophid parasitoids attacking leafminers (Heinz and Parrella, 1989; Ho and Ueno, 2002). Hosts are not the only resources for successful reproduction. Other non-host food like nectar and honeydew also plays an important role in parasitoid reproductive success (Jervis *et al.*, 1993; Godfray, 1994; Jervis and Kidd, 1996; Olson *et al.*, 2000). Eulophid parasitoids of leaf miners including *H. varicornis* require carbohydrate sources. Provision of sugar solution can commonly increase female longevity (Syme, 1977; Foster and Ruesink, 1984; Jervis and Kidd, 1996; England and Evans, 1997; Idris and Grafius, 1997; Rojas *et al.*, 1998; Schmale *et al.*, 2001). Thus, in order to improve mass-rearing efficiency, it is ideal to develop a laboratory food for adult parasitoids that contains proteins, carbohydrates, vitamins, etc. Studies of nutritional physiology in parasitoids would contribute greatly to improvement of the efficiency.

Because of direct implications for biological control, many studies in parasitoids have focused on foraging for host insects (e.g. Godfray, 1994; Quicke, 1997). These studies have contributed to a better understanding of how parasitoids find their hosts and have revealed the importance of their presence for reducing pest populations in agricultural systems. However, hosts are not the only resource for successful reproduction of parasitoids. Other needs, such as food, should play an important role in their reproductive success. The presence and availability of food for adult parasitoids in agricultural systems thus can affect the success of biological control, and studies of nutritional physiology in parasitoids would then contribute to the understanding of the importance of parasitoid food in biological control (van Emden, 1990; Heimpel and Jervis, 2005).

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