Reproductive fitness of *Diadegma semiclausum* Hellen (Hymenoptera: Ichneumonidae) in response to host density

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Abstract *Diadegma semiclausum* is an important larval parasitoid of diamondback moth (DBM), *Plutella xylostella*. The present study investigated the reproductive fitness of *D. semiclausum* females in response to host densities of 5 and 30 DBM larvae per cabbage seedling per day. Both the number of hosts parasitised and the number of female progeny produced over the life of the parasitoid were significantly greater in the 30 than the 5 host density (hosts parasitised: 601 ± 31 versus 120 ± 15 and female progeny produced: 67 ± 10 versus 12 ± 2) ($P < 0.0001$). In the high host density, the daily number of hosts parasitised and proportion of female progeny produced significantly increased from 3–4 days until 20–22 days after oviposition started, after which time these parameters significantly decreased ($P < 0.0001$). The implication of these results for mass-rearing and field release is discussed.

Keywords *Diadegma semiclausum*, *Plutella xylostella*, host density, female progeny, parasitism.

INTRODUCTION

The impact of a parasitoid on its host population depends upon its ability to find and parasitise hosts and to increase the number of its offspring when needed (Waage & Hassell 1982; Mackauer 1983). The spatial patterns of parasitism by insect parasitoids, and the importance of these to the population dynamics of host-parasitoid interactions, have been topics of widespread interest amongst pure and applied ecologists. Many models have been developed, among which heterogeneity in the distribution of parasitism has played an important part in population regulation (Hassell & May 1973, 1974; Murdoch & Oaten 1975). However, the potential effects of host density on other aspects of reproductive

behaviour have usually been neglected. Apart from parasitism, few studies have noted the effect of host density on the reproductive rate (Liu 1985), sex allocation (Sandlan 1979; Asante & Danthanarayana 1993; He et al. 2006) and longevity (Ellers et al. 2000) of the ovipositing parasitoids. An understanding of the influence of host density on the reproductive fitness of parasitoids may have a direct application in biological control programmes.

Diadegma semiclausum (Hymenoptera: Ichneumonidae) is one of the most important larval parasitoids of the diamondback moth (DBM), *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) (Waterhouse & Norris 1987; Talekar

& Shelton 1993). Host density-dependent behaviour has been reported in this species (Legaspi & Legaspi 2005). However, whether host density affects life history traits, in particular longevity, sex ratio, reproductive period and parasitism of the parasitoid, is unknown. The present study aimed to investigate the effect of host density on the aforementioned life history traits of *D. semiclausum*.

MATERIALS AND METHODS

The breeding colonies of DBM and *D. semiclausum* were started from DBM larvae collected from a commercial farm in Palmerston North in January 2008. The insects were maintained at the Entomology and IPM Laboratory, Massey University, at $21\pm1^{\circ}\text{C}$, 16:8 h (light:dark) (high-frequency, broad-spectrum Biolux tubes, Osram, Germany) and $50\pm10\%$ RH. All experiments were carried out under these environmental conditions.

DBM were reared on potted cabbage plants (Summerglobe hybrid, *Brassica oleracea* var *capitata*) in Plexiglas cages (30×30×30 cm) with two holes (13 cm in diameter) made on opposite sides and covered with a metal mesh (aperture size = 0.25 mm) for ventilation. One side of the cage was fitted with a circular opening (16 cm in diameter) for handling plants and insects in the cage. Twenty newly emerged DBM adults (10 males and 10 females) were released into a Plexiglas cage containing a potted 6 to 8 week old cabbage seedling. After 24 h, the seedling together with the DBM eggs was transferred into a transparent plastic chamber (25 cm in height × 17 cm in diameter). A circular metal frame covered with a nylon net (aperture size of the mesh = 0.25mm) was kept on the top of the chamber in order to prevent the newly emerged larvae from moving away from the plant.

To maintain the parasitoid colony, a mated parasitoid female was released into a plastic chamber with a cabbage seedling along with 10 3rd and 4th instar DBM larvae. After 24 h, the parasitoid was removed and parasitized DBM larvae were reared on the same infested seedling until pupation in a plastic container (10 cm in height × 8.5 cm in diameter) with two circular

holes (5 cm in diameter) covered with fine metal mesh. Pupae were collected and maintained in individual glass vials (7.5 cm in height × 2.5 cm in diameter) until emergence. Both DBM and parasitoid adults were fed with 10% honey solution soaked in cotton balls (0.5 cm in diameter).

Two host densities (5 or 30 3rd instar DBM larvae per cabbage seedling per day) were set up in this experiment. DBM larvae were transferred to cabbage seedlings using a fine, soft brush 6 h before the experiment. Mated 3-day-old parasitoid females were individually released into a plastic chamber containing a cabbage seedling infested by host larvae. After 24 h in the chamber, each parasitoid was removed and transferred to a new seedling infested by the same number of larvae. This process was repeated until the parasitoid died (up to 38 days). There were 10 and 9 female parasitoids tested for host densities of 5 and 30 larvae, respectively. The number of cocoons (= parasitised DBM larvae) was recorded daily for each parasitoid. Emerged parasitoid adults were sexed (adult females have a long and sharp ovipositor). The percent parasitism (number of cocoons/total number of hosts) was calculated. Dead parasitoids were dissected to count the number of mature eggs remaining in their ovaries.

All non-proportional data were analysed using ANOVA, with proportional data being arcsine transformed before ANOVA. Regression analyses were employed to determine the relationship between the number of DBM larvae parasitised or proportion of female progeny and the parasitoid age since the initiation of oviposition. Data for each female individual were pooled for regressions but only means ($\pm$ SEs) are presented (Figures 1 & 2). The missing DBM larvae in some replicates were excluded in data analysis.

RESULTS

The total number of host larvae parasitised and female progeny produced were significantly greater in the density of 30 DBM larvae ($P<0.0001$) but percent parasitism was significantly greater in host density of 5 larvae ($P<0.0001$) (Table 1). Host density had no

Table 1 Reproductive fitness parameters of *D. semiclausum* over their lifetime when exposed to 5 or 30 DBM larvae per day.

	Host density	
	5	30
Total no. hosts parasitised	120.3±15.0 b ¹	601.0±31.1 a
Parasitism (%)	95.8±0.8 a	78.3±4.3 b
Total no. female progeny	11.6±2.4 b	67.4±9.8 a
Female progeny (%)	12.2±3.0 a	12.1±1.5 a
Egg load at death	30.1±3.9 a	28.9±3.9 a

¹Means (±SEs) followed by the same letter in each row are not significantly different ($P>0.05$).

significant effect on proportion of female progeny produced and egg load at death ($P>0.05$) (Table 1).

At the host density of 5 DBM larvae, the number of DBM larvae parasitised and the proportion of female progeny were not significantly affected by female parasitoid age ($P>0.05$) (Figures 1a & 2a).

However, at a density of 30 DBM larvae, the number of DBM larvae parasitised and proportion of female progeny significantly increased during the first few days, reached a maximum during the second week ($P<0.0001$) and declined thereafter ($P<0.0001$) (Figures 1b & 2b).

Figure 1 Mean number of DBM larvae parasitised during the oviposition period of females at host densities of (a) 5 DBM larvae and (b) 30 DBM larvae per cabbage seedling per day.

Figure 2 Mean percent female parasitoid progeny produced during the oviposition period of females at host densities of (a) 5 DBM larvae and (b) 30 DBM larvae per cabbage seedling per day.

DISCUSSION

Similar to results reported by Legaspi & Legaspi (2005), density-dependent parasitism was not detected for *D. semiclausum* in this study. Indeed, in 171 cases of parasitoid oviposition reviewed by Stiling (1987), density-dependent parasitism occurred in only 25% cases. One of the common reasons cited for density-independent parasitism is egg limitation in the searching parasitoids (Smith & Maelzer 1986). In the present study, a number of eggs still remained in the ovaries of dead parasitoids at both densities (Table 1) and females are able to continually develop eggs during their life (i.e. strongly synovigenic) (Khatri et al. 2009), suggesting that *D. semiclausum* females may not suffer egg limitation. To some extent lower percent parasitism at high host density may be a result of parasitoids spending more

time handling hosts and overcoming defences (Wang & Keller 2004).

Progeny sex ratio dynamics in response to host density occurs in many parasitoid species (Sandlan 1979; Asante & Danthanarayana 1993; Ferreira De Almeida et al. 2002; He et al. 2006). In *Aphidius ervi* (Hymenoptera: Aphidiidae), the proportion of female progeny increases with an increase in host density from 15 to 50 pea aphids (He et al. 2006). While the proportion of female progeny is almost the same (12%) in both host densities of *D. semiclausum* (Table 1), more female progeny are produced at the higher host density (Table 1) and a synchronisation of oviposition (number of hosts parasitised, Figure 1b) and sperm release (proportion of female progeny, Figure 2b) is detected. This could be attributed to the assumption that increased host

encounter may stimulate females to lay eggs by activating a synchronised release of sperm and eggs (Flanders 1946).

Sex allocation in parasitoids is known to be maternal age dependent (King 2000). The present study shows that the sex allocation patterns were different between the two host densities (Figures 2a & 2b). At higher host density the sharp decline of female progeny in the later stage of the parasitoids' life (Figure 2b) may be due to sperm depletion (King 2000; Santolamazza-Carbone et al. 2007). The different patterns of sex allocation in *D. semiclausum* suggest that this species can adjust the fertilisation strategy in response to host density.

The present study shows that reproductive fitness of *D. semiclausum* females can be increased by rearing them at higher host densities as they parasitise more larvae and produce more female offspring under such conditions. Ovipositing adults parasitise most larvae and produce more female offspring during the first 3 weeks of the oviposition period, suggesting that using females up to that stage could help optimise *D. semiclausum* mass-rearing programmes.

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