OVIPOSITION STRATEGY OF *APHIDIUS ERVI* (HYMENOPTERA: APHIDIIDAE) IN RESPONSE TO HOST DENSITY

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ABSTRACT

The reproductive response of *Aphidius ervi* Haliday to the density of pea aphid, *Acyrtosiphon pisum* (Harris), was investigated in plastic cylinders (10.5 cm high × 8.5 cm diameter). Mean number of aphids parasitised and eggs laid by a single *A. ervi* significantly increased with an increase of host density. Numbers of eggs laid per parasitoid reached a plateau at host densities of 75 aphids/cylinder and above. However, the number of eggs laid in each parasitised aphid significantly decreased (from 2.9 to 1.3 eggs) with the increase of host density from 15 to 75 aphids/cylinder, after which no further decrease occurred. These results suggest that the parasitoid adjusts oviposition strategy in response to increasing host density through increasing parasitism and decreasing superparasitism. The proportion of female progeny developed from fertilised eggs increased (up to 70%) with the increase of host density from 15 to 50 or 75 aphids/cylinder, after which it gradually declined, suggesting that the sperm limit occurs when host density reaches 50 to 75 aphids/cylinder.

Keywords: *Aphidius ervi*, host density, reproduction, sex allocation, *Acyrtosiphon pisum*.

INTRODUCTION

Hymenopterous parasitoids of aphids have provided spectacular success in biological control (Starý et al. 1988). The impact of a parasitoid on its host population greatly depends upon its ability to find and parasitise hosts and to increase offspring numbers in response to increasing host density (Waage & Hassell 1982; Mackauer 1983). It is important to identify the form of the parasitoid response to prey density in population modelling, from which biological control programmes can be developed (Mills & Lacan 2004). In analytical host-parasitoid models, changes in the density-dependent sex ratio of parasitoids influence the level of host population equilibrium and the stability of the host-parasitoid relationships thus affecting the success of biological control (Waage & Hassell 1982; Hassell & Waage 1984).

Aphidius ervi Haliday is a cosmopolitan, solitary, endophagous parasitoid (Marsh 1977) and a major biological control agent of several aphid species on economically important crops such as legumes and cereals (Powell 1982; Starý et al. 1988). Ives et al. (1999) studied some aspects of the functional response of *A. ervi* on pea aphid, *Acyrtosiphon pisum* (Harris), with emphasis on the parasitoid's behavioural decisions and their influence on the parasitism rate. In this paper, the relationship between host density and reproductive fitness of *A. ervi* was investigated by determining how host density affected parasitoid reproductive output and sex allocation. The aim was to provide further information for the assessment and improvement of *A. ervi*'s effectiveness in biological control.

MATERIALS AND METHODS

Insects and experimental conditions

A breeding colony of *A. ervi* was established from parasitised blue-green lucerne aphid, *Acyrtosiphon kondoi* Shinji, collected on lucerne in Palmerston North, New Zealand, in December 2002. The colony was subsequently reared on pea aphid, feeding on potted broad bean, *Vicia faba* L. cv. Pride, for five generations before being used for experiments. All experiments were carried out in transparent plastic cylinders (8.5 cm in diameter, 10.5 cm in height) with gauze-covered holes in the top and sides for ventilation. A broad bean cutting standing in a plastic container (6.5 cm in diameter, 8.5 cm in height) with tap water was placed in the plastic cylinder and replaced when wilted. Honey solution (10%) was supplied daily in a cotton wool wick (1 cm in length), inserted through a hole (0.6 cm in diameter) in the top of the cylinder. Parasitoid adults used for the experiments emerged from pea aphids parasitised at third instar. The experiment was carried at $20 \pm 1^\circ\text{C}$ and 60–70% RH with 16:8 h light:dark.

Experiment

To determine whether and to what extent host density affected reproduction of *A. ervi*, six densities of aphids (15, 25, 50, 75, 100 and 125 third instars/cylinder/parasitoid female/day) were tested, with 10 replicates for each density. One mated *A. ervi* female (<12 h old) was introduced into an experimental cylinder with aphids feeding on a bean plant cutting. The female was allowed to stay in the cylinder for 24 h, and then moved to another cylinder with the same number of healthy third instar aphids, etc. until she died.

Because superparasitism was common under laboratory conditions, the oviposition potential of *A. ervi* was estimated by counting both the number of eggs laid (fecundity) and aphids parasitised (parasitism). To estimate the daily number of eggs laid in a parasitised aphid, five aphids from each cylinder at densities of 15 and 25 aphids, 10 aphids at density of 50 aphids, and 20 aphids at densities of 75, 100 and 125 aphids were randomly selected from each cylinder 4 days after the removal of the female parasitoid. These selected aphids were dissected in 70% alcohol under the stereomicroscope (Leica MZ12, Germany). The numbers of parasitoid larvae recorded from dissecting were assumed equal to the number of eggs laid (Bueno et al. 1993). The remaining aphids were reared until mummification. The number of eggs laid was assumed equal to the total number of aphids parasitised (= the sum of mummies and aphids parasitised detected by dissecting) $\times$ the average number of eggs laid in a parasitised aphid detected by dissecting. The emerged offspring were counted and sexed.

Statistical analysis

Goodness of fit tests were used to test whether the data were normally-distributed. Effect of aphid density on the number of parasitoid eggs laid was assessed by one-way ANOVA and means separated by Tukey's studentised range (HSD) test. Data for percent female progeny, parasitism rate and eggs per parasitised aphid were not normally distributed after transformation and were thus analysed using the nonparametric Kruskal-Wallis test. Means were subsequently separated by Dunn's procedure for multiple comparisons (Zar 1999). A significance level of $P < 0.05$ was used for all tests.

In this study, more than 80% of eggs were laid within the first 8 days, thus all data presented were from the first 8 days.

RESULTS

Mean number of aphids parasitised and eggs laid (actual fecundity) during *A. ervi* females' life time increased with the increase of host density ($P < 0.0001$) (Fig. 1). Fecundity reached a plateau at host densities of 75/cylinder and above (Fig. 1). The number of eggs laid in each parasitised aphid decreased with the increase of host density from 15 to 75/cylinder, after which no further decrease occurred ($P < 0.0001$) (Fig. 2). The daily parasitism rate decreased when the host density increased to 50/cylinder ($P < 0.0001$) (Fig. 3). The proportion of female progeny was greatest at host densities of 25 to 100/cylinder, and least at extremes of low and high host densities ($P < 0.0001$) (Fig. 4).

FIGURE 1: Mean number of aphids parasitised and eggs laid by *A. ervi* at different host densities (15, 25, 50, 75, 100 and 125 aphids/cylinder). Within the same category (Aphids parasitised or Eggs laid) columns with the same letters are not significantly different (Kruskal-Wallis test for aphids parasitised and ANOVA for eggs laid at $P>0.05$). Error bars are SEM.

FIGURE 2: Mean number of eggs per parasitised aphid laid by *A. ervi* at different host densities. Columns with the same letters are not significantly different (Kruskal-Wallis test at $P>0.05$). Error bars are SEM.

FIGURE 3: Mean daily parasitism rate of *A. ervi* at different host densities. Columns with the same letters are not significantly different (Kruskal-Wallis test at $P>0.05$). Error bars are SEM.

FIGURE 4: Mean proportion of female progeny of *A. ervi* at different host densities. Columns with the same letters are not significantly different (Kruskal-Wallis test at $P>0.05$). Error bars are SEM.

DISCUSSION

High fecundity and parasitism rates are considered necessary for parasitoids to be able to respond rapidly to the increases in pest density (Waage & Hassell 1982; Waage 1990). The results of the present study indicate that *A. ervi* can adjust oviposition strategy in response to increasing host density through increasing parasitism and decreasing superparasitism (Figs 1 & 2). These data alone suggest that this parasitoid has high potential to suppress the aphid population when the latter increases. However, when the host population was 50/cylinder, mean daily parasitism rate significantly decreased (Fig. 3). The behaviour of *A. ervi* in this experiment is consistent with the classic Holling type II functional response (Holling 1959), i.e. the number of aphids parasitised increased with an increase in aphid density but at a progressively decreasing rate. A type II functional response was also found in some other *Aphidius* species, such as the *A. smithi* Sharma & Subba Rao (Mackauer 1983) and *A. sonchi* Marshall (Liu 1985). Results of this study suggest that a host density equivalent to 50 aphids/cylinder is the highest critical density where the parasitoid could maximise its control efficiency. This information could be important when considering host-parasitoid density ratio in biological control programmes (Hassell & Waage 1984). For example, to maximise biological control efficiency of pea aphids, parasitoids could be released at a rate of about one female parasitoid/50 aphids.

The proportion of female progeny developed from fertilised eggs quickly and significantly increased with the increase of host density from 15 to 50 aphids/cylinder, after which it gradually declined. This suggests that the highest potential proportion of female progeny that *A. ervi* can produce is about 70% and sperm limit occurs when host density reaches 50 to 75 aphids/cylinder. Offspring sex ratio of other *Aphidius* species, such as *A. smithi* (Mackauer 1983) and *A. sonchi* (Liu 1985), has also been found to vary with host density. In hymenopteran parasitoids, males can mate several times while females mate only once. It is thus to the female's benefit that she produces the minimum number of males possible. However, when hosts occur at low density, a high parasitoid female sex ratio should reduce the ability of parasitoid persistence (Tripathi & Singh 1991), leading to extinction of the host population and eventually the parasitoid population. This suggests that the female parasitoids can adjust the sex allocation strategy in response to the host density. A similar case was found in *Aphelinus mali* Hal, which attacks the woolly apple aphid (Mueller et al. 1992).

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