Host feeding and oviposition strategy of *Eretmocerus warrae* (Aphelinidae: Hymenoptera) under different host densities

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Abstract *Eretmocerus warrae* Naumann & Schmidt is a thelytokous parasitoid of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood). In conditions of $22\pm1^{\circ}\text{C}$, $60\pm5\%$ RH and 16:8 h light:dark, the host feeding and oviposition strategy of *E. warrae* under seven host densities (20, 40, 60, 80, 100, 120 and 140 whitefly nymphs) was investigated. With an increase in host density the number of nymphs parasitised and fed upon by *E. warrae* significantly increased, but the percentage of nymphs parasitised, superparasitised and fed on significantly decreased ($P<0.0001$). The parasitoid longevity significantly increased with an increase in host density up to 100 nymphs ($P<0.0001$). These results suggest that *E. warrae* can adjust its feeding and oviposition strategy according to the host availability, and can potentially contribute to biological control of greenhouse whitefly.

Keywords *Eretmocerus warrae*, host density, fecundity, host feeding, parasitism, *Trialeurodes vaporariorum*.

INTRODUCTION

The greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood), is an important pest, causing serious economic damage to crops throughout tropical and subtropical regions and in glasshouses (Byrne et al. 1990). The sessile nymphs of *T. vaporariorum* have been successfully managed in glasshouse systems with parasitoids (Vet et al. 1980; Gerling et al. 1990). Among the *Eretmocerus* species that have been reared from *T. vaporariorum* (Zolnerowich & Rose 2008), *E. warrae* Nauman & Schmidt is a newly described thelytokous (no males) species (de Barro et al. 2000). It was first found in greenhouses in Auckland, New Zealand, in 1997 (Workman et al.

2008). This species is a pro-synovigenic parasitoid because its ovaries contain a limited number of mature eggs and it continues to feed on hosts and mature eggs throughout its life (Hanan et al. 2010).

Parasitoid response to varying host density is an important parameter for measuring the parasitoid-host dynamics (Holling 1959). Understanding this in a parasitoid-host system can help evaluate the potential of a parasitoid for maintaining the host population (Murdoch & Briggs 1996). Hymenopteran parasitoids can increase their fecundity and alter the sex ratio of their progeny in response to host density (Waage

& Hassell 1982; Wang & Keller 2005). For example, *Aphidius ervi* Haliday, a parasitoid of pea aphid, parasitises a higher number of hosts and allocates a higher proportion of female progeny in response to higher host densities (He et al. 2006). However, in parasitoid species that use their hosts for both oviposition and feeding (Jervis & Kidd 1986; Heimpel & Collier 1996), the decision to oviposit or feed is manipulated by several factors depending upon the host and parasitoid itself (Lauzière et al. 1999). Egg load, maturation delay and life expectancy are parasitoid-related, while host quality and quantity are host-related factors (Sahragard et al. 1991; Rosenheim & Rosen 1992; Heimpel & Collier 1996; Videllet et al. 1997). Some studies suggest that host feeding is density-dependent and the proportion of hosts fed upon by a parasitoid decreases with increasing host density (Kidd & Jervis 1989). However, other studies demonstrate that host feeding is density-independent (Sahragard et al. 1991; van Lenteren et al. 1996) and oviposition is density-dependent where parasitoids respond positively to increasing host densities (Lauzière et al. 1999).

So far, little is known about the host feeding and oviposition strategy of *E. warrae* in response to the density of *T. vaporariorum*. The objective of this study was to investigate the influence of host density on fecundity, host feeding, parasitism, superparasitism and longevity of *E. warrae*. The information generated here would help optimise mass-rearing procedures and field release rates of *E. warrae* against whiteflies.

MATERIALS AND METHODS

Breeding colony and experimental conditions

The colonies of *T. vaporariorum* and *E. warrae* were initiated with parasitised and unparasitised pupae of *T. vaporariorum* obtained from BioForce Limited, Auckland, New Zealand. 'Moneymaker' tomato plants were used for rearing the colonies. *Trialeurodes vaporariorum* and *E. warrae* were maintained and all experiments carried out at $22 \pm 1^\circ\text{C}$ with $60 \pm 5\%$ RH and 16:8 h light:dark, in the laboratory. All parasitoids used in this study emerged from *T. vaporariorum* that were parasitised at the second or third instar.

Experiments

To determine whether and how host density affected host feeding, fecundity, parasitism and longevity of *E. warrae*, seven host densities were set up: 20, 40, 60, 80, 100, 120 and 140 second instar nymphs of *T. vaporariorum* per female *E. warrae*. Ten adult females (ten replicates) were used for each treatment. For each replicate, one female parasitoid (<12 h after adult emergence) was released into a Petri dish (5.5 cm in diameter $\times$ 1.3 cm in height) with a fresh leaf infested by a test number of nymphs, allowed to stay for 24 h, and then moved into another Petri dish containing the same number of nymphs. This process was repeated until she died. As *E. warrae* place their eggs between the venter of nymphs and leaf surface (Hanan et al. 2009; 2010), all nymphs were turned over to determine the presence or absence of eggs under the stereomicroscope (Leica MZ12, Germany). The daily and life time oviposition and host feeding patterns were determined by counting the numbers of eggs laid and hosts fed upon by the parasitoid. Host feeding was recorded if the nymph body fluid was found to have effused as a result of penetration of the female ovipositor into the vasiform orifice of host nymphs (Hanan et al. 2010). The longevity of adult parasitoids was also recorded.

Statistical analysis

A goodness-of-fit test was used to test data normality. All data were normally distributed, thus analysed using ANOVA followed by Tukey's test. The percentage data were arcsine transformed prior to analysis but non-transformed means are presented.

RESULTS AND DISCUSSION

Egg load, host stage and host availability influence the oviposition and host feeding behaviour of many parasitoid species (Rosenheim & Rosen 1992; Heimpel & Collier 1996; Videllet et al. 1997; Hansen & Jensen 2002). The present study shows that with the increase in host density *E. warrae* laid more eggs, lived longer, and parasitised and fed on more whiteflies ($P < 0.0001$) (Figure 1). These results suggest that at higher host densities

parasitoids obtain energy by feeding on hosts, which enables greater egg development and maturation as well as prolonged longevity. Sahragard et al. (1991) also report that in *Dicondylus indianus* Olmi (Hymenoptera: Dryindinae) increased fecundity at higher host densities is a positive function of increased longevity. Furthermore, host haemolymph fed on by adult parasitoids may provide lipids and

carbohydrates necessary for higher fecundity and enable greater longevity of adult parasitoids as reported for *Eupelmus vuilletti* (Crawford) (Hymenoptera: Eupelmidae) (Giron et al. 2004).

In the present experiment with *E. warrae*, the proportion of hosts fed on, parasitised and superparasitised was significantly higher in lower host densities of 20 and 40 nymphs than in higher host densities of 60–140 nymphs ($P < 0.0001$) (Figure 2). This pattern is consistent with a type II functional response (Holling 1959), which is also found for *A. ervi* (He et al. 2006), *E. mundus* Mercet (Zandi-Sohani et al. 2008) and *Encarsia acaudaleyrodis* Hayat (Shishehbor & Zandi-Sohani 2011). These results suggest that

Figure 1 Mean ($\pm$ SEM) values for (a) number of eggs laid, (b) hosts parasitised, (c) hosts fed on and (d) longevity as an adult, in *E. warrae* exposed to different host densities. Columns with the same letters are not significantly different ($P > 0.05$).

Figure 2 Mean ($\pm$ SEM) percentage of hosts (a) fed on, (b) superparasitised and (c) parasitised, by *E. warrae* exposed to different host densities. Columns with the same letters are not significantly different ($P > 0.05$).

E. warrae can adjust its feeding and oviposition strategy according to host availability.

The present results imply that *E. warrae* can contribute to the biological control of greenhouse whitefly because it significantly increases its fecundity and the number of whiteflies parasitised and fed on with an increase in host density. However, the highest parasitism and host feeding rates are found when the host density is 20 nymphs, suggesting that 20 *T. vaporariorum* nymphs per *E. warrae* adult is a good starting point for determining the optimal rearing density and release rate for augmentative biological releases.

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