HOST AGE PREFERENCE IN *APHIDIUS ERVI* (HYMENOPTERA: APHIDIIDAE)

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ABSTRACT

Host age preference by *Aphidius ervi* Haliday on pea aphid, *Acyrthosiphon pisum* (Harris), and the effects of host age on *A. ervi* reproductive fitness and sex allocation were studied in the laboratory. *Aphidius ervi* preferred aphids that were 3-5 days old over the younger (1 and 2 days old) and older (6 and 7 days old) aphids for oviposition. The body size and egg load at emergence of *A. ervi* progenies significantly increased with the increase of host age at the time of parasitisation from 1 to 4 days old, after which no further increase occurred. The results support the size-dependent sex ratio theory that *A. ervi* deposits fertilised eggs in large hosts and unfertilised eggs in small ones. The potential impact of the host age preference on biological control is discussed.

Keywords: *Aphidius ervi*, age, preference, body size, sex allocation, *Acyrthosiphon pisum*.

INTRODUCTION

Many studies have demonstrated that parasitism can influence development, fecundity, and population growth of the host aphids (Tsai & Wang 2002; Lin & Ives 2003; He et al. 2005). Generally, aphids parasitised in early instars are mummified before reaching reproductive maturity, whereas those parasitised in late instars are able to reach adult stage and produce progeny. Therefore, the parasitoid impact on the aphid population growth largely depends on the pattern of the host age selected for parasitisation (Hågvar & Hofsvang 1991; Tsai & Wang 2002) and host age preference is critical to the success of biological control of aphids (Tsai & Wang 2002).

Foraging parasitoids usually encounter hosts of different ages or sizes and have opportunities to select the most suitable hosts to maximise their reproductive fitness. For some solitary species of parasitoids, hosts selected for oviposition are determined by host size (Kouamé & Mackauer 1991) because large hosts contain more resources for parasitoid progeny development than small hosts (Charnov et al. 1981; Liu 1985). Many studies suggest that host size preference by parasitoids affect their progeny fitness, such as the body size (Liu 1985; Lampson et al. 1996) and egg load at emergence (Liu 1985; Mills & Kuhlmann 2000). Host age may also affect sex allocation of parasitoids (Godfray 1994). According to Charnov et al. (1981) and Charnov (1982), parasitoids can make efficient use of the size variation in the hosts encountered by allocating fertilised diploid eggs to large hosts and unfertilized eggs to small ones.

Aphidius ervi Haliday is a cosmopolitan endophagous parasitoid (Marsh 1977) of several aphid species on economically important crops such as legumes and cereals (Starý 1978; Powell 1982). Previous studies have demonstrated that the impact of *A. ervi* on population growth of the pea aphid, *Acyrthosiphon pisum* (Harris), largely depends on the host age at parasitism (He et al. 2005), and body size of pea aphid is positively correlated with its age (Sequeira & Mackauer 1992). However, so far little is known about the host age preference by *A. ervi*. Knowledge of host preference would lead to a better understanding of the population dynamics of the host and parasitoid (Nechols &

Kikuchi 1985). Therefore, to provide useful information for the development of biological control strategies, this study investigated the host age preference by *A. ervi* and its effect on the reproductive fitness and sexual allocation.

MATERIALS AND METHODS

Insects and experimental conditions

A breeding colony was started from *A. ervi* that emerged from blue-green lucerne aphid, *Acyrthosiphon kondoi* Shinji, collected on lucerne in Palmerston North, New Zealand, in December 2002. The colony was 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, one in the top (5 cm in diameter) and two (2 cm in diameter) in opposite sides for ventilation at 20±1°C and 60-70% RH with 16:8 h light:dark. 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 the third instar.

Experiment

To determine host age preference by *A. ervi* in relation to host age and its effect on *A. ervi* reproduction, mated females were supplied with host aphids of different ages, from 1 to 7 days old. Ten females (replicates) were tested in this experiment. For each replicate, one mated female parasitoid (< 12 h old) was introduced into an above-mentioned plastic cylinder with 105 healthy aphids (15 aphids of each age class) 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 105 healthy aphids, etc. until she died. After the removal of the female parasitoid, aphids of different age classes were separated and transferred to an uninfested bean plant in a cylinder.

To estimate the number of eggs laid, five aphids of each age class were randomly selected from each cylinder 4 days after the removal of the female parasitoid, and dissected in 70% alcohol under a stereomicroscope (Leica MZ12, Germany). The number of parasitoid larvae recorded from dissecting was assumed equal to the number of eggs laid (Bueno et al. 1993). The remaining aphids were reared until mummification. The emerged progeny were counted and sexed.

To determine the effect of host age preference on reproductive fitness of parasitoids, the body size was measured and the egg load of newly emerged parasitoids from each host age class was determined. The head width (a measure of body size) of 30 newly emerged progeny of each sex randomly selected from each host age class was measured using the above stereomicroscope. The egg load of parasitoid females at emergence was determined by dissecting 30 newly emerged females randomly selected from each host age class. They were dissected in 70% alcohol on a slide under the above stereomicroscope. One drop of acid fuchsin was added to the alcohol and allowed to stand for 3–5 min for staining. The number of eggs in the ovaries was counted under a compound microscope (Olympus, Japan).

Statistical analysis

A goodness of fit test was used to test the distribution of data before analysis. Data of the number of egg load were not normally distributed even after transformation and thus analysed using the nonparametric Kruskal-Wallis test followed by Dunn's procedure for multiple comparisons (Zar 1999). Other data were normally distributed and analysed using ANOVA followed by a Tukey's studentized range test. Data of proportion of female offspring were arcsine transformed prior to analysis. The relationship between body size and egg load of newly emerged females was analysed using an analysis of regression.

RESULTS

Aphidius ervi females significantly preferred aphids that were 3-5 days old for oviposition with significantly higher number of aphids parasitised (Fig. 1) and eggs laid (Fig. 2) (P<0.0001).

Host age also had significant effect on proportion of female progeny produced (P<0.0001), which was highest in 6-day-old aphids and lowest in 1-day-old aphids (Fig. 3).

The head width of newly emerged adults of both sexes significantly increased with the increasing host age (from 1 to 4 days old) at the time of parasitisation (P<0.0001) (Table 1). Regardless of the host age when parasitised, females were significantly larger than males (P<0.01) (Table 1). The egg load of newly emerged females was also significantly higher when parasitoids attacked aphids that were 3-7 days old (P<0.0001) (Fig. 4). There was a positive linear relationship between the body size and egg load of newly emerged females (P<0.0001) (Fig. 5).

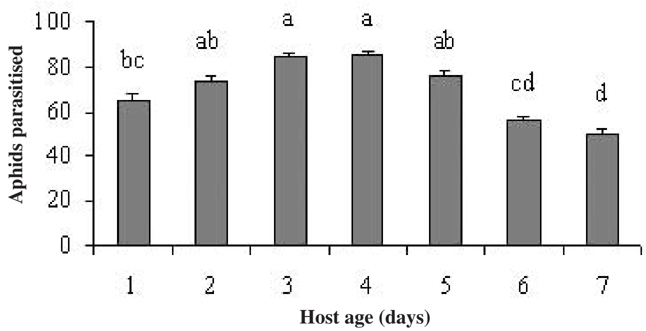

FIGURE 1: Mean number of aphids parasitised per *A. ervi* female in relation to host age. Columns with the same letters are not significantly different (P>0.05).

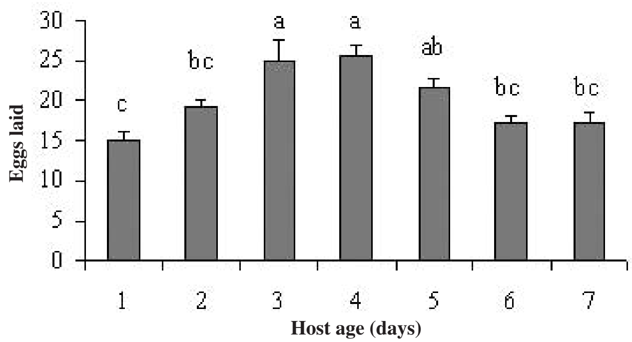

FIGURE 2: Mean number of eggs laid per *A. ervi* female (estimated from dissection) in relation to host age. Columns with the same letters are not significantly different (P>0.05).

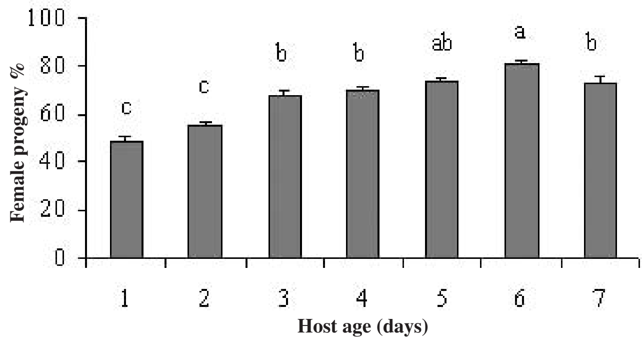

FIGURE 3: **Mean proportion of female progeny emerged from hosts of different age classes. Columns with the same letters are not significantly different (P>0.05).**

TABLE 1: **Mean (± SE) head width (mm) of newly emerged *A. ervi.* Means followed by the same letters within rows were not significantly different (P>0.05).**

	Host age (days) at parasitisation						
Sex	1	2	3	4	5	6	7
Male	0.535 d ± 0.0034	0.556 c ± 0.0032	0.580 b ± 0.0031	0.601 a ± 0.0037	0.599 a ± 0.0045	0.596 ab ± 0.0049	0.598 a ± 0.0051
Female	0.585 d ± 0.0027	0.613 c ± 0.0032	0.642 b ± 0.0031	0.660 a ± 0.0037	0.656 ab ± 0.0029	0.646 ab ± 0.0054	0.649 ab ± 0.0059

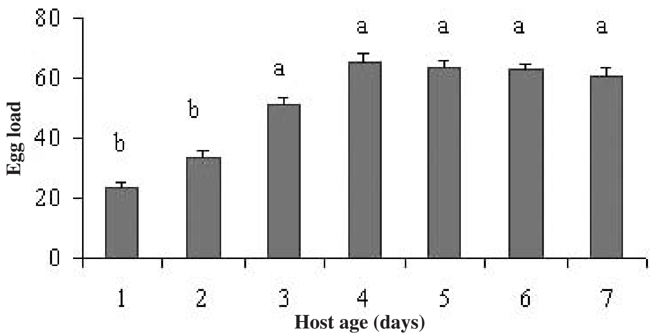

FIGURE 4: **Mean egg load per female progeny emerged from hosts of different age classes. Columns with the same letters are not significantly different (P>0.05).**

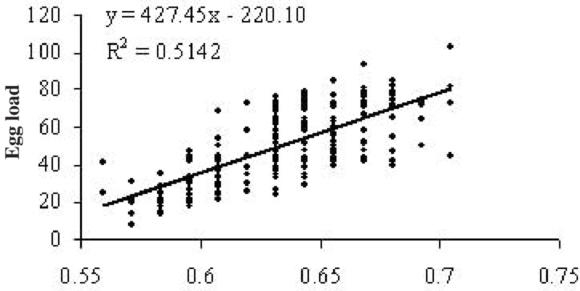

FIGURE 5: Relationship between body size and egg load per newly emerged female of *A. ervi*.

DISCUSSION

Female *A. ervi* attacked pea aphids of different ages. The immature pea aphids grow in size as they develop to adult stage and larger aphids have more food resource for *A. ervi* larvae (Li et al. 2002; He et al. 2005). According to the theory of optimal host acceptance in parasitoids, which is based on the model of optimal diet in predators (Stephens & Krebs 1986), *A. ervi* should prefer older aphids for oviposition. However, older aphids may be more capable of physically defending themselves from parasitisation and cost more to the female parasitoids in oviposition (Chau & Mackauer 2001). The present results indicate that *A. ervi* preferred aphids that were 3-5 days old over the younger (1-3 days old) and older ones (6-7 days old) for oviposition. Therefore, the food resource at the point of oviposition is not the only factor that determines the oviposition decision by parasitoids, and the parasitoids may select hosts according to the optimal trade-off between food supply and oviposition costs.

The results in this study also indicate that host age preference by *A. ervi* is related to its progeny's reproductive fitness. The body size of progeny and egg load of newly emerged females were similar when aphids were attacked at 4-7 days old, suggesting that the quantity and quality of food resource for the parasitoid progeny are similar in aphids of this age range.

The increase in proportion of female progeny of *A. ervi* with host size supports the host size-dependent sex allocation theory in parasitic Hymenoptera (Charnov et al. 1981; Charnov 1982). There is also field evidence that host instar plays a role in sex ratios, as reported for *A. ervi* parasitising pea aphid, where a male-biased population emerged from small aphids in the early season (Sequeira & Mackauer 1993).

Although the body size of parasitoids emerged from aphids parasitised at 4 days old was similar to that emerged from aphids parasitised at 6 days old, the proportion of female offspring was significantly lower when parasitoids selected 4-day-old aphids for oviposition than that when parasitoids selected 6-day-old aphids. Sex ratio data suggest that the body size of hosts at the point of oviposition is the major factor affecting the sex allocation by *A. ervi*.

The findings of this study have implications for laboratory mass rearing and field release of *A. ervi*. For example, aphids that are 3-5 days old appear to be the most appropriate hosts in the mass-rearing program because they gave the best fitness return for the parasitoids. The timing for field release of the parasitoids should be set to when the 3- to 5-day-old aphids are most abundant because parasitism in these age-classes produces no or few aphid progenies (He et al. 2005) and gives a greater parasitoid population of better reproductive fitness in the next generation.

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REFERENCES

Bueno BHP, Gutierrez AP, Ruggle P 1993. Parasitism by *Aphidius ervi* (Hym.: Aphidiidae): preference for pea aphid and blue alfalfa aphid (Hom.: Aphididae) and competition with *A. smithi*. Entomophaga 38: 273-284.

Charnov EL 1982. The theory of sex allocation. Princeton University Press, Princeton, NJ. 355 pp.

Charnov EL, Hartogh RL, Los-den Jones WT, van den Assem J 1981. Sex ratio evolution in a variable environment. Nature 289: 27-33.

Chau A, Mackauer M 2001. Host-instar selection in the aphid parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae): assessing costs and benefits. Canadian Entomologist 133: 549-564.

Godfray HCJ 1994. Parasitoids: behavioral and evolutionary ecology. Princeton University Press, Princeton, New Jersey. 473 pp.

Hågvar EB, Hofsvang T 1991. Aphid parasitoids (Hymenoptera, Aphidiidae): biology, host selection and use in biological control. Biocontrol News and Information 12: 13-41.

He XZ, Wang Q, Teulon DAJ 2005. The effect of parasitism by *Aphidius ervi* on development and reproduction of the pea aphid, *Acyrthosiphon pisum*. New Zealand Plant Protection 58: 202-207.

Kouamé KL, Mackauer M 1991. Influence of aphid size, age and behaviour on host choice by the parasitoid wasp *Ephedrus californicus*: a test of host-size models. Oecologia 88: 197-203.

Lampson LJ, Morse JG, Luck RF 1996. Host selection, sex allocation, and host feeding by *Metaphycus helvolus* (Hymenoptera: Encyrtidae) on *Saissetia oleae* (Homoptera: Coccidae) and its effect on parasitoid size, sex, and quality. Environmental Entomology 25: 283-294.

Li S, Falabella P, Giannantonio S, Fanti P, Battaglia D, Digilio MC, Volkl W, Sloggett JJ, Weisser W, Pennacchio F 2002. Pea aphid clonal resistance to the endophagous parasitoid *Aphidius ervi*. Journal of Insect Physiology 48: 971-980.

Lin LA, Ives AR 2003. The effect of parasitoid host-size preference on host population growth rates: an example of *Aphidius colemani* and *Aphis glycines*. Ecological Entomology 28: 542-550.

Liu SS 1985. Aspects of the numerical and functional responses of the aphid parasite, *Aphidius sonchi*, in the laboratory. Entomologia Experimentalis et Applicata 37: 247-256.

Marsh PM 1977. Notes on the taxonomy and nomenclature of *Aphidius* species (Hym.: Aphididae) parasitic on the pea aphid in North America. Entomophaga 22: 365-372.

Mills NJ, Kuhlmann U 2000. The relationship between egg load and fecundity among *Trichogramma parasitoids*. Ecological Entomology 25: 315-324.

Nechols JR, Kikuchi RS 1985. Host selection of the spherical mealybug (Homoptera: Pseudococcidae) by *Anagyrus indicus* (Hymenoptera: Encyrtidae): influence of host stage on parasitoid oviposition, development, sex ratio, and survival. Environmental Entomology 14: 32-37.

Powell W 1982. The identification of hymenopterous parasitoids attacking cereal aphids in Britain. Systematic Entomology 7: 465-473.

Sequeira R, Mackauer M 1992. Covariance of adult size and development time in the parasitoid wasp *Aphidius ervi* in relation to the size of its host, *Acyrthosiphon pisum*. Evolutionary Ecology 6: 34-44.

Sequeira R, Mackauer M 1993. Seasonal variation in body size and offspring sex ratio in field populations of the parasitoid wasp, *Aphidius ervi* (Hymenoptera: Aphidiidae). Oikos 68: 340-346.

Starý P 1978. Seasonal relations between lucerne, red clover, wheat and barley agro-ecosystems through the aphids and parasitoids (Homoptera, Aphididae; Hymenoptera, Aphidiidae). Acta Entomologica Bohemoslovaca 75: 296-311.

Stephens DW, Krebs JR 1986. Foraging theory. Princeton, New Jersey. 247 pp.

Tsai JH, Wang JJ 2002. Host age choice for parasitism by *Lysiphlebia mirzai* and its effect on the development and reproduction of brown citrus aphid. BioControl 47: 645–655.

Zar JH 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, NJ,USA. 663 pp.