



Fitness gain in a koinobiont parasitoid *Diaeretiella rapae* (Hymenoptera: Aphidiidae) by parasitising hosts of different ages

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ABSTRACT

Host age-dependent fitness of *Diaeretiella rapae* was studied on cabbage aphid *Brevicoryne brassicae*. When given a choice of nymphs of four different ages (1, 3, 5 and 7 days), females showed a strong preference for oviposition in older nymphs, which were also the largest in the body size, and left the majority of younger nymphs unparasitised. More than 70% of offspring emerged from 5-day and 7-day old parasitised nymphs. Parasitoids develop faster in older hosts than in younger hosts. Development time of males was shorter than females in older hosts, but the development time of males and females was similar in younger hosts. The body size of adult *D. rapae* was positively correlated with the age of the hosts in which they developed. The sex ratio of offspring was found to be female-biased. A higher proportion of females emerged from older hosts. *D. rapae* females emerged from older hosts lived significantly longer. The potential fecundity of the females emerged from older (larger in body size) hosts was significantly greater than of those emerged from younger hosts with smaller bodies. Results suggest that *D. rapae* preferred older hosts to maximise the reproductive fitness gain. The oviposition strategy of *D. rapae* is discussed in the context of efficiency of this parasitoid in biological control programmes.

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Introduction

Cabbage aphid *Brevicoryne brassicae* (L.) (Homoptera: Aphididae) is a worldwide pest of forage, horticultural crops and oil-seed crucifers (Singh and Ellis, 1993). It is considered to be the most serious pest of brassicas such as cauliflower, cabbage, broccoli and brussels sprouts, and has a history of destroying entire crops of turnip, rape and swede (*Brassica napus*) in New Zealand (Lammerin and Morice, 1970). Direct feeding by the aphid causes yellowing, wilting, distortion and stunting of infested plants. In addition, this aphid transmits more than 20 different plant viruses, including cauliflower mosaic virus (CaMV) and turnip mosaic virus (TuMV) (Broadbent, 1957) that result in economically important diseases of crucifers. Cabbage aphid reproduces both sexually and asexually and its population increases very quickly. In New Zealand, the aphid generally reproduces parthenogenetically, overwinters in the egg stage and completes more than 15 generations per year.

A number of pesticides are used for control of these aphids. However, these tend to have a short-term effect because of the short aphid generation time, and severe pesticide toxicity to their natural enemies (Xu et al., 2009). Moreover, the aphid has developed resistance

to several commonly used pesticides (Clark and Yamaguchi, 2002). Biological control and Integrated Pest Management (IPM) provide an alternative option for suppressing the aphid populations.

Diaeretiella rapae (M'Intosh) (Hymenoptera: Aphidiidae) is a solitary endoparasitoid of more than 60 different aphid species (Pike et al., 1999). The most common hosts of *D. rapae* in Australia, New Zealand and in other countries are cabbage aphid, green peach aphid *Myzus persicae* (Sulzer) and mustard aphid *Lipaphis erysimi* (Kaltenbach) (Carver and Stary, 1974), and it is a potential candidate for suppressing cabbage aphid populations (George, 1957). In the USA, *D. rapae* has been used in classical and augmentative biological control of Russian wheat aphid *Diuraphis noxia* (Mordvilko) (Bernal and Gonzalez, 1993). The parasitoid was deliberately introduced to Australia for controlling cabbage aphid (Carver and Stary, 1974). *D. rapae* is of Western Palaearctic origin and has been accidentally introduced, and established, in New Zealand (Carver and Stary, 1974), but little attention has been given to it as a potential biological control agent of aphid pests.

When parasitoids locate their hosts, they make a series of oviposition decisions in order to maximise their fitness gain (Godfray, 1994), which include the number of eggs to lay, ratio of fertilised and unfertilised eggs and whether to superparasitise the host or not. The decisions made by a parasitoid are affected by the quality of the hosts it encounters, and host quality generally depends on its age and size. As in many Hymenopteran species, females develop from fertilised eggs and males develop from

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unfertilised eggs (haplodiploidy) in *D. rapae*. A foraging mother thus controls the sex of her offspring and can produce sons before mating. Because sex ratio directly affects the population dynamics of the species, decisions made on sex allocation are crucial, have strong fitness outcomes and, therefore, have evolutionary implications. In the case of pro-ovigenic species (such as *D. rapae*), which have a limited number of eggs, the oviposition decision is perhaps more crucial than in synovigenic species in which females can produce eggs throughout life. Oviposition decisions of parasitoids vary as some species are attracted to larger hosts (Charnov et al., 1981; Waage, 1982; Godfray, 1994), some to smaller or intermediate hosts, or are indiscriminate of host body size (Jones, 1982; Hare and Luck, 1991; Bernal et al., 1998). The parasitoid should attack the best quality hosts and avoid those in which successful larval development is doubtful. *D. rapae* is a koinobiont parasitoid (Zhang and Hassan, 2003) where host paralysis is transient and sometimes absent, allowing hosts to continue development after parasitism. Thus, the resources available for the developing koinobiont parasitoid are not fixed. Previous studies indicated that female *D. rapae* select older (larger) cabbage aphid nymphs for oviposition (Kant et al., 2008) but the reasons behind that behaviour have not been tested.

The purpose of the present study is to examine the effects of *D. rapae* oviposition preferences by comparing the fitness parameters of adults emerged from four different age groups of cabbage aphid nymphs. The results of this study will be useful in developing biological control strategies for cabbage aphid using *D. rapae*, to overcome the low population of *D. rapae* in the early spring in New Zealand (Kant et al., 2010).

Materials and methods

Parasitised and unparasitised cabbage aphids were collected from a commercial cauliflower field in Palmerston North, New Zealand. The colonies of the host and the parasitoid were established and maintained in laboratory conditions at 22 ± 2 °C, 60–70% RH and 16 h (L) photoperiod. The aphids were reared on cabbage seedlings (cultivar “Autumn Pride”) in ventilated plexiglass cages (30×30×30 cm). Parasitised aphid mummies were removed from plants and were kept individually in 2 ml microcentrifuge tubes until adult emergence. The emerged *D. rapae* were sexed under a stereomicroscope (Leica MZ12), paired for mating in a glass vial and fed 10% honey solution.

In the first experiment, mated females (n=15) were given a choice of different ages of cabbage aphid nymphs (1, 3, 5 and 7-day old). The nymphs of these ages were selected as representatives of different sizes. Age of the cabbage aphid nymphs was positively correlated to their size. Fifty adult aphids were transferred to a fresh plant and allowed to produce nymphs for 24 h before adults were removed. The nymphs were allowed to develop until they reached the required age for the experiments. Ten aphids each of age 1 day-old and 5-day old were transferred to a cabbage seedling and ten nymphs each of age 3-day old and 7 day-old aphids were transferred to another cabbage seedling. The aphids were allowed to settle on the plants and both plants were placed in an oviposition arena, a cage similar to described above. In each case the older nymphs were readily distinguished from the younger ones. A mated female was released into the oviposition arena for 24 h, then transferred to a new oviposition arena with the same configuration of aphids, again for 24 h. This process was repeated until the death of the female.

After parasitism, each age group of aphid nymphs was allowed to develop on individual cabbage seedling. The more easily handled older nymphs were transferred to separate cabbage seedlings, leaving the younger nymphs. Once the parasitised aphids were mummified, they were transferred to individual 2 ml microcentrifuge tubes and kept until adult emergence. The emerged *D. rapae* were sexed and their body length was measured. To measure the body length, the insects were dissected, and head, thorax and abdomen were placed on a

glass slide in saline solution. The length of each tagmata was measured as maximal length in dorsal aspect using calibrated eyepiece micrometre. The measurements were then added together. The potential fecundity of the newly emerged females from nymphs of different age groups was estimated by dissecting their ovaries and counting the number of eggs. A subset of adults was fed with 10% honey solution and their longevity was observed.

In the second set of experiments the 1, 3, 5 and 7-day old aphids were dissected 4 days after being parasitised and the growth of the developing parasitoid larvae was estimated by measuring their head width. Those dissected aphids which contained more than one parasitoid larva were not used for measuring the larval size.

Statistical analyses

Data on immature development time, adult body size, adult longevity and egg load of *D. rapae* were normally distributed (goodness-of-fit test) and were analysed using analysis of variance (ANOVA). The means were separated using a Tukey’s studentised range (HSD) test. The percentage data of adults emergence from hosts of different ages were arcsine transformed prior to ANOVA. Regression analysis was used to identify the relationship between host age and the size of parasitoid larvae, and between host age and the size of adult parasitoids. The sex ratio of the offspring were analysed by Chi square test. All analyses were carried out at $\alpha = 0.05$ level of significance.

Results

Oviposition by *D. rapae* females in hosts of different ages

D. rapae emerged from all parasitised cabbage aphid nymphs regardless of their age group. A greater number of 7-day old cabbage aphid nymphs were parasitised by *D. rapae* compared to the younger nymphs. About 70% of all aphid mummies collected resulted from parasitism of the older hosts (5 and 7 days old) ($F_{3, 56} = 9.33$, $P < 0.001$). The number of mummified aphids collected from 1-day and 3-day old hosts did not differ significantly (Fig. 1).

Immature development time in different hosts

Development time, from egg to adult, of male and female parasitoids varied with the age of the host in which they developed. In younger hosts, females took significantly longer to develop than males ($F_{7, 186} = 17.94$, $P < 0.001$). However, in older hosts the development time of males and females was not different (Fig. 2). Females developed significantly quicker in older hosts, while males took about the same

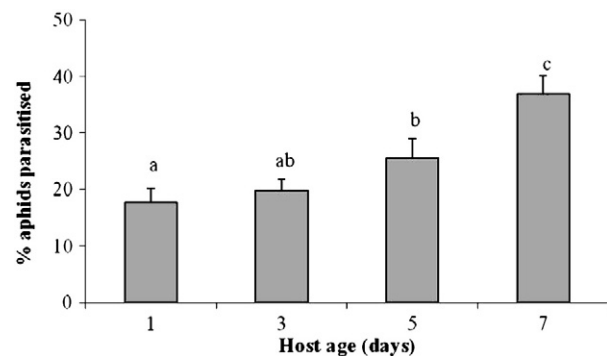


Fig. 1. Percentage of cabbage aphids parasitised by *Diaeretiella rapae* when offered nymphs of different age in a choice test. Means with the same letters are not significantly different (Tukey’s HSD $P < 0.05$), error bars represent the standard error.

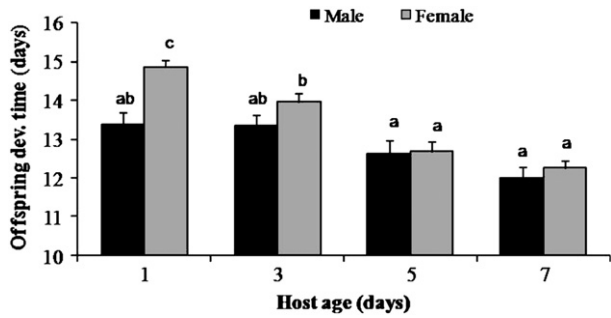


Fig. 2. Development time, from oviposition to adult emergence, of male and female *Diaretiella rapae* offspring in cabbage aphid nymphs parasitised at four different ages. Means with the same letters are not significantly different (Tukey's HSD $P < 0.05$), error bars represent the standard error.

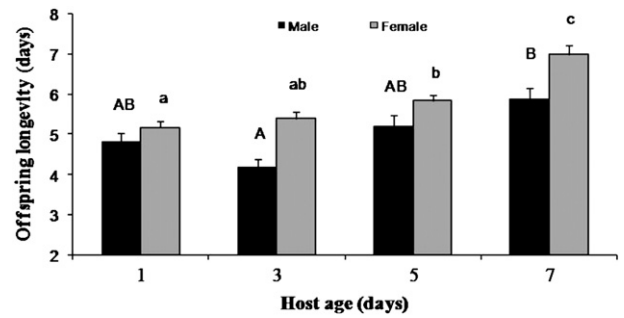


Fig. 4. Longevity (mean \pm SE) of male and female *Diaretiella rapae* emerged from cabbage aphid parasitised at different ages. Means with the same letters are not significantly different (Tukey's HSD $P < 0.05$).

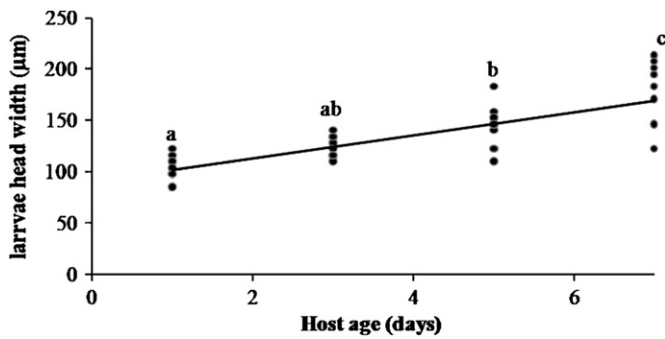


Fig. 3. Relationship between the head width of developing *Diaretiella rapae* larvae after 4 days of parasitism and the age of host at the time of parasitism. Means with the same letters are not significantly different (Tukey's HSD, $P < 0.05$).

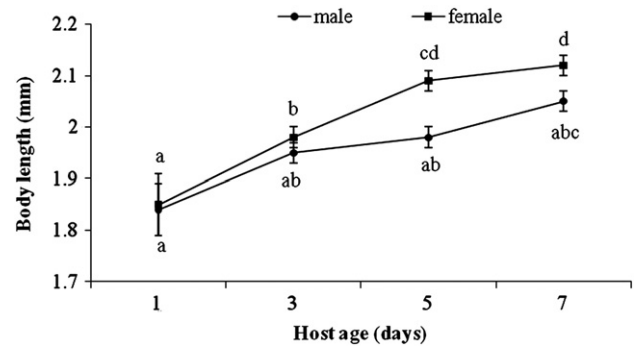


Fig. 5. Body length (mean \pm SE) of male and female *Diaretiella rapae* emerged from cabbage aphid parasitised at different ages. Means with the same letters are not significantly different (Tukey's HSD $P < 0.05$).

time to develop into adults regardless of host age, although development time in older hosts was lower (Fig. 2).

Variation in the growth of parasitoid larvae developing in different age hosts appeared four days after oviposition. A positive correlation was observed between larval size and host age at the time of oviposition ($R^2 = 0.57$, $F_{1, 59} = 59.91$, $P < 0.0001$). The larvae developing in 7-day old hosts were larger than the larvae developing in other hosts ($F_{3, 44} = 20.63$, $P < 0.001$; Fig. 3).

Sex ratio of D. rapae offspring emerged from hosts of different ages

Significantly more females than males emerged from aphids parasitised at 5 and 7-days old ($P < 0.01$). The numbers of males and females emerged from hosts parasitised at 1 and 3 days old were not significantly different ($P > 0.05$). Overall, female-biased progeny emerged from all age groups of hosts (Table 1).

Longevity of D. rapae emerged from hosts of different ages

Parasitoids emerged from older hosts lived significantly longer than those emerged from younger hosts. The effect was most apparent in females that emerged from 7-day old hosts ($F_{3, 90} = 6.12$, $P < 0.001$) (Fig. 4). Females from the 5-day old hosts also lived longer than those

emerged from 1-day hosts. However, no significant difference was found in the longevity of females emerged from 1-day versus 3-day or 3-day versus 5-day old hosts (Fig. 4). Male longevity was similar irrespective of the host age, except the males emerged from 7-day old hosts lived longer than the males emerged from 3-day old hosts ($P = 0.01$) (Fig. 4).

Body size of the offspring emerged from hosts of different ages

The body size of adult *D. rapae* was positively correlated with the age of their host. Variation in body size was most apparent in female offspring when all host age groups were analysed ($F_{3, 34} = 15.49$, $P < 0.001$). Females that emerged from 3-day old hosts were larger than those emerged from 1-day old hosts, however, the size difference in females that had emerged from 5-day old and 7-day old hosts was

Table 1
Female/male sex ratio of the *Diaretiella rapae* offspring emerged from hosts of different ages. Columns with the same letters are not significantly different ($P > 0.05$).

Offspring	1 day old	3 day old	5 day old	7 day old	Combined
Female	29 a	24 a	40 b	46 b	139
Male	21 a	18 a	24 a	17 a	80
Sex ratio	1.38	1.33	1.67	2.7	1.74
χ^2 value at $\alpha = 0.05$	1.28	0.8	4	13.35	15.89

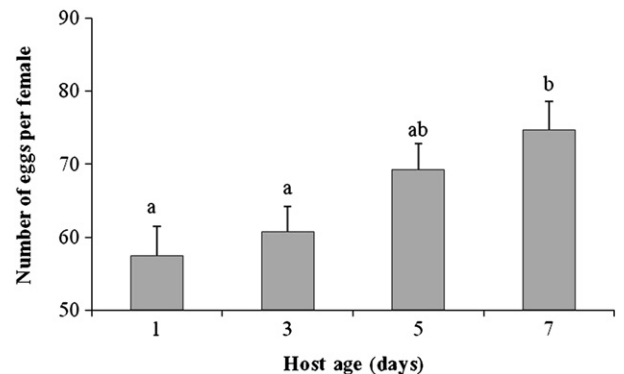


Fig. 6. Egg load (mean \pm SE) of female *Diaretiella rapae* emerged from cabbage aphid hosts parasitised at different ages. Means with the same letters are not significantly different (Tukey's HSD $P < 0.05$).

not significant (Fig. 5). The size of males emerged from different age hosts was not significantly different (Fig. 5).

Egg-load of female offspring emerged from hosts of different ages

The mean number of eggs found in the ovaries of females newly emerged from 7-day old hosts was significantly greater than in females emerged from 1-day and 3-day old hosts (Fig. 6). There was no significant difference in the egg load of females emerged from 1-day, 3-day and 5-day old hosts (Fig. 6).

Discussion

Unlike predators, which often feed on many prey individuals before achieving maturity, parasitoids are dependent on nutrition available in a single host for their complete development. Therefore, selection of a high quality host is very important. *D. rapae* left the majority of younger and thus, smaller, hosts unparasitised. Most of the parasitoids emerged from older, larger hosts. This preference for larger hosts is consistent with observations of other parasitoid species (Elzinga et al., 2003; Harvey et al., 2004; Sandanayaka et al., 2009). This relationship makes sense if host size provides an indication of the amount of resources available to the developing larvae (Charnov, 1982; Islam and Copland, 1997; Bennett and Hoffmann, 1998), and the quality of food available to the immature stages has a strong influence on the physical and physiological traits of the adult (Vinson and Iwantsch, 1980; Jervis et al., 2008), which is consistent with the theory of optimal host acceptance (Stephens and Krebs, 1986).

In contrast to our observations, the parasitoid *Monoctonus paulensis* (Ashmead) selects younger, smaller pea aphid nymphs amongst those available (Chau and Mackauer, 2000). It has been proposed that defensive behaviour of hosts that correlates with their age/size also influences host selection (Chau and Mackauer, 2000), resulting in a trade-off between quality and defensive behaviour of a host (Godfray, 1994). He and Wang (2006) suggested that the pea aphid parasitoid *Aphidius ervi* (Haliday) selected medium size hosts over smaller and larger ones to optimise the trade-off between lower nutrient levels in smaller hosts, and a stronger defensive behaviour of larger hosts. Defensive behaviours such as kicking, body shaking and walking away have been observed in older cabbage aphid nymphs when *D. rapae* attacks them (R. Kant, unpublished data) but this appears to be insufficient to prevent more frequent attacks on larger cabbage aphid nymphs and, commonly, deposition of more than one egg per individual (Kant et al., 2008).

The benefits of oviposition in larger hosts are readily apparent in the growth and development of immature *D. rapae*. The first instar larvae in older hosts were significantly larger in size, and female adults developed quicker than in younger hosts, suggesting that more nutrients were available in larger host and that nutritional quality of nymphs increases with their age. However, the developmental time of males did not differ between larger and smaller hosts, probably because the quality and quantity of nutrients available in smaller hosts were sufficient for the development of male *D. rapae*, which are smaller than the females. Sequeira and Mackauer (1992) found that nutritional requirements of males and females vary in *A. ervi*. Similarly, Jarosik et al. (2003) found that females of *Aphidius colemani* (Viereck), another aphid parasitoid, grew bigger than males in the same size hosts.

Parasitoids can increase their reproductive fitness by reducing development time (Harvey and Strand, 2002). Rapid development increases the fitness of *D. rapae* males by increasing their chances of finding virgin females for mating (Kant and Sandanayaka, 2009). In some species, males wait near the female mummies for their emergence to mate at the earliest opportunity (Werren, 1980). Females also benefit from early mating, as this allows them to have more of their eggs fertilised. Males of *D. rapae* mate several times in their life, whilst females mate once (Kant, 2009), therefore, male *D. rapae* increase their fitness by having multiple matings if they develop faster.

Further, we found that *D. rapae* larvae developing in 7-day old aphid nymphs grew faster than in 5-day old nymphs, but the body size of emerging adults was not different. This could be because the instant resources available to the parasitoid larvae were greater in 7-day than in 5-day old hosts, the quantity of resources was sufficient in both host ages.

Longer life of parasitoids emerged from larger hosts indicates another potential fitness gain in *D. rapae*. Longevity of *D. rapae* adults showed a positive correlation with their size. By living longer, females may encounter and parasitise more hosts. In contrast, males who can inseminate up to 6 females a day (Kant, 2009) may become sperm-depleted quickly. This suggests that male *D. rapae* have evolved to maximise early mating opportunities, rather than having a protracted mating period. However, it has also been found that female *D. rapae* become sperm-depleted if their male mate had previously mated 3 or more times; multiply-mated males appear to be sperm-depleted (R. Kant, unpublished data). Although males gain fitness by maximising mating frequency, females may lose fitness if mated with a sperm-depleted male.

Host age significantly affected the sex allocation decision of *D. rapae*. Females manipulated the sex ratio of offspring by allocating the majority of unfertilised eggs (producing males) to younger hosts, and fertilised eggs (producing females) to the older ones. The increased proportion of female offspring emerging from older hosts supports the hostquality-dependent sex allocation model in parasitic hymenopterans (Charnov et al., 1981). By allocating male eggs to larger hosts, female *D. rapae* underutilise the resources, whilst allocating female eggs to smaller hosts reduces fitness by yielding smaller females that live significantly shorter time and have significantly fewer eggs. There is also increase in mortality of females developing in smaller hosts (Jarosik et al., 2003), which would contribute to the shift in sex ratio toward males. Thus, foraging females maximise resource use and thus the quality of offspring by regulating the release of sperm from their spermatheca on the basis of the quality of host they encounter at the time of oviposition.

Parasitism of older hosts also increases the chances of survival and successful emergence of *D. rapae* adults. Both idiobiont and koinobiont parasitoid females may gain fitness by parasitising the hosts that allow quick development of the offspring. The longer the parasitised host is active, the greater is the chance of host, and thus developing parasitoid, mortality by predators. Similarly, developing parasitoid larvae are vulnerable to multiple- and hyperparasitism. The chances of parasitoid larval mortality may, therefore, be significantly higher in younger/smaller hosts. Thus, there is a significant impact of host selection decision on the likelihood of offspring mortality via predation, hyperparasitism and pesticide use. By ovipositing fertilised eggs in larger hosts, *D. rapae* reduces the chances of mortality of its offspring, because the offspring takes less time to develop.

The study suggests that by parasitising older hosts, *D. rapae* increase their fitness by increasing the chances of successful emergence of offspring and producing more female offspring. For the purpose of biological control, production of more, larger and longer-lived females is beneficial because it is the females that are directly responsible for controlling the pest population. Similarly, the sex ratio has important effect on biocontrol potential of parasitoids (Ode and Hardy, 2008). The results suggest that production of more females can be achieved by selection of older host aphids during their mass production. As cabbage aphid populations naturally increase faster than *D. rapae* populations in spring (Kant et al., 2010), inundation with *D. rapae* during spring may help in suppressing the initial cabbage aphid population in the glasshouse or in the field.

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