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Body size and fitness relation in male and female *Diaeretiella rapae*

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Abstract A strong relationship exists between body size and fitness in parasitoids. However, it is unclear whether the relationship is symmetric or asymmetric in males and females. The present study investigated the body size and fitness relationship in *Diaeretiella rapae* emerged from small and large nymphs of cabbage aphid *Brevicoryne brassicae*. A positive relationship existed between the size of the aphid host and growth of parasitoid larva developing in it. The fitness gain in males and females was not proportionate to their body size gain. Females mated with larger males produced 10 % more female offspring than females mated with smaller males. However, females that developed in large hosts produced 62 % more offspring (total male and female) than the females emerged from smaller hosts. The findings suggest that the number of offspring and the progeny sex ratio were affected by the body size of both male and female *D. rapae*.

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Introduction

Body size in insects is an important trait that affects fitness of individuals (Henry et al. 2009). The quantity of resources consumed by individuals during ontogenesis is directly related to their final body size (Godfray 1994). Size varies continuously due to the effects of natural selection on resource acquisition (Chown and Gaston 2010). Thus, body size and fitness in organisms influence their efficiency in acquiring resources (van Alphen and Visser 1990). However, the scope of resource acquisition by an individual is finite in some insects, while others can acquire as much as they can subject to availability of the hosts. For example, predators can consume varying number of prey for their growth and development, while resources available to developing parasitoids are fixed by their solitary host. Idiobiont parasitoids completely paralyse their hosts during oviposition which stops the host's growth and development. Thus, the developing parasitoid larvae have a strictly fixed resource. However, koinobiont parasitoids allow their hosts to feed and grow, therefore, their host resources could be dynamic in nature (Sequeira and Mackauer 1992; Wyckhuys et al. 2008) if the host continues to feed.

In parasitoids, both the quality and quantity of resources available to larvae are important for their overall growth and development (Sequeira and Mackauer 1992; Harvey and Strand 2002). Larger hosts are generally considered better than smaller ones, because they provide more resources to the developing larvae (Mackauer 1986). Resources gained by parasitoid larvae are the main (capital) resources that determine the future reproductive efficiency of parasitoids during their adult life (Jervis and Kidd 1986).

The quantity of resources immediately available to a newly hatched parasitoid larva (instant resources) depends on the size of the host in which oviposition occurred. Therefore, adult parasitoids might consider the size of potential hosts during oviposition, irrespective of their foraging habit as idiobiont or koinobiont (Godfray 1994). Furthermore, host selection should favour the strategy that utilises limited resources more efficiently. Another critical question is whether ovipositing female should be selective in allocating the sex of its offspring. Studies have found that in parasitoid species where sex of offspring can be facultatively controlled by the mother before oviposition, females allocate fertilised eggs (female offspring) to good quality hosts and unfertilised (male) eggs to lower quality hosts (Charnov et al. 1981; Wyckhuys et al. 2008; Kant et al. 2012a). This is evident when the female has a choice of different quality hosts, but how does the female behave if she encounters hosts of uniform quality—either all large (high quality) or all small hosts?

Optimal foraging and game theories (Stephens and Krebs 1986; Hammerstein and Selten 1994; Perry and Pianka 1997) predict that natural selection will favour parasitoid behaviour that maximises their fitness. If a foraging female shows a preference for allocating fertilised eggs to hosts of a certain size, it indicates that there are fitness consequences (Charnov 1982). Behavioural preferences of females in terms of reproductive fitness gain can be tested experimentally. This study examines a comparative reproductive fitness gain in male and female *Diaeretiella rapae* (Hymenoptera: Aphidiidae). *Diaeretiella rapae* is an endoparasitoid of cabbage aphid *Brevicoryne brassicae* (Hemiptera: Aphididae) and several other aphids attacking cruciferous and non-cruciferous plants (Pike et al. 1999). Female *D. rapae* emerge with matured eggs (Bernal and González 1997) and prefer to oviposit after mating (Kant et al. 2012c). The mated females prefer to oviposit into larger (older) aphid nymphs, despite oviposition in the larger hosts requiring longer host-handling time and more energy (higher number of probes per host) (Kant et al. 2008). The benefit of time- and energy-consuming oviposition in larger hosts is the quicker development and higher longevity of adults emerged from these hosts (Kant et al. 2012a). Differences in body size of male and female *D. rapae* have been found in an uncontrolled open system (Kant et al. 2012b) as well as in controlled laboratory conditions (Kant et al. 2012a). In the wild population, 79 % of mating male *D. rapae* were smaller than their female partner (Kant et al. 2012b). However, it is still unclear whether the relationship between parasitoid body size and fitness is similar or asymmetric in male and female *D. rapae*. Morris and Fellowes (2002) suggested that the relationship between fitness and size is stronger in female parasitoids.

The current study estimated the size-fitness relationship in *D. rapae* by considering the following aspects: (1) larval growth and body size of male and female *D. rapae* developed in small and large cabbage aphid nymphs, (2) the relationship between host size and resource allocation in parasitoid larvae, (3) the effect of body size of mating pairs on offspring number and sex ratio.

Materials and methods

Insect colonies

Colonies of cabbage aphid, *B. brassicae* and its parasitoid *D. rapae* were established from a commercial cauliflower field near Palmerston North, Manawatu, New Zealand. Insects were reared in laboratory on cabbage seedlings (cultivar: ‘Autumn pride’) in 30 × 30 × 30 cm plexiglass cages. The colonies were maintained at 22 ± 2 °C, 60–70 % RH and 16 h light photoperiod.

Oviposition and sex allocation by *D. rapae* in a no-choice test

Cabbage aphid nymphs of two age groups, small 1–2 day old and large 6–7 day old, were offered separately to mated, 1–2 day old, 10 % honey-fed *D. rapae* females. Size of cabbage aphid nymphs is positively correlated to their age (Kant et al. 2008). Each female was offered 30 nymphs of a particular size for 24 h for four consecutive days. The parasitised aphids were transferred to cabbage leaves for their development and were observed daily for mummification. Each mummified aphid was transferred to an individual microfuge tube until emergence of adult parasitoid. Male and female *D. rapae* emerged from small and large aphids were measured.

The insects were first killed by freezing and then preserved in 70 % ethanol. 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 tagma was measured as maximal length in dorsal aspect using calibrated eyepiece micrometer. The measurements were then added together. To simplify this process, and to find the adequate substitute for body size measurement, the body size of *D. rapae* adults was regressed against their hind tibia length, wing length and head width. The hind tibia length was highly correlated to the total body length of *D. rapae* adults (body length $= 3.54x + 0.139$, $R^2 = 0.83$, where $x =$ hind tibia length). Therefore, hind tibia length was used to estimate the size of adults in the rest of the experiments. Ten females were tested in each group.

Resource allocation to *D. rapae* larvae developing in small and large hosts

A separate experiment was used to assess the growth of larvae in small and large hosts. Parasitised aphids were transferred to cabbage leaves and after four days of parasitism the aphids were dissected under a microscope. The size of each larva was quantified by measuring the width of its head capsule. Twenty larvae were dissected from each small and large size hosts.

We developed a resource allocation index (RAI) to compare the amount of host resources (nutrients) allocated to the *D. rapae* larvae after four-day of parasitism until *D. rapae* larvae undergo pupation in the hosts. Therefore, RAI indicates the growth of larvae during the period from four-day old larvae to adults, while developing in either large or small hosts.

$$\mathrm{RAI} = (\mathrm{HTL} - \mathrm{MHW})/\mathrm{HTL}$$

As larval size and adult size could not be measured on the same *D. rapae* individual, the average size of four-day old larvae in small and large hosts (quantified as mean head width, MHW) was substituted for actual larval measurements. The size of emerging adults was measured as hind tibia length (HTL). The index was calculated individually for all males and females that emerged from large and small hosts. Mean RAI was compared for males and females emerged from large and small hosts.

Reproductive fitness of large and small *D. rapae*

The parasitoids obtained from the previous experiments were used to determine their reproductive gain. Adults emerged from one to two day old aphid nymphs were considered “small” and those emerged from five to six day old aphids were considered “large”. Four mating combinations were tested: (1) small male × small female, (2) small male × large female, (3) large male × small female, and (4) large male × large female. In each case a male and a female were paired in a small vial (7.5 cm height × 2.5 cm diameter) for mating. Each pair was offered 10 % honey solution and left in the glass vial for 24 h. Each mated female was offered 30 cabbage aphids (5–6 days old nymphs) on a cabbage seedling in a cage for 24 h every day until the death of the female. For each mating combination, ten pairs were tested.

The parasitised aphids were transferred to a new cabbage plant for development. Once the aphids were mummified, they were transferred to individual vials until the adult parasitoids emerged. The number of mummies and offspring resulted from each mating were counted. The total number of offspring (adults emerged) was used as a fitness criterion for females. The number of female offspring was used as a fitness criterion for males.

Body size gain and reproductive gain in male and female *D. rapae*

Body size gain in male and female *D. rapae* was calculated as relative increase in their body size when they developed in large hosts (5–6 day old) compared to small hosts (1–2 day old). Reproductive gain of female *D. rapae* is the relative increase in the number of offspring (combined male and female offspring) produced by females emerged from large hosts compared to small hosts. Reproductive gain in male *D. rapae* is the relative increase in the number of female offspring produced by females mating with large males compared to offspring produced by females mating with small males.

Statistical analysis

Analysis of variance (PROC GLM, SAS 9.2) was used to analyse differences in the means, including the number of adults and number of females emerged from small and large size hosts, body size mating combinations, hind tibia length of male and female, and differences in the RAI in large and small hosts. When the overall results were significant, the differences among treatments were compared using Tukey's studentised (HSD) test. Ordinary least squares regression was used to examine the relationship between hind tibia length and body size of adult parasitoids. Sex ratios were analysed using binary logistic regression (PROC LOGISTIC, SAS 9.2). All analyses were carried out at $\alpha = 0.05$ level of significance.

Results

Oviposition and sex allocation by *D. rapae* in a no-choice test

In a no-choice test, the number of aphids parasitised by female *D. rapae* per day during the four day oviposition period did not differ whether the females were offered small or large aphid nymphs ($F_{1,18} = 0.57$; $P = 0.46$) (Fig. 1). A significantly higher proportion of females (74.5 %) emerged from larger hosts (logistic regression: $\chi^2 = 32.86$, df = 1, $P < 0.001$), while the same proportion of males and females emerged from smaller hosts (logistic regression: $\chi^2 = 1.47$, df = 1, $P = 0.22$).

Body size gain in *D. rapae* larvae and adults

The size of *D. rapae* larvae found in the dissected cabbage aphid nymphs was positively correlated to the size of the nymph [$y = 0.106x + 11.22$, where $y =$ larval head width (μm) and $x =$ aphid body length (μm)] ($R^2 = 52.1$, $P = 0.002$). The mean (±SE) head width of the *D. rapae* larvae at four days after oviposition was larger in large hosts (156.9 ± 4.8 μm) than in small hosts (117.7 ± 5.6 μm) ($F_{1,46} = 28.31$, $P < 0.001$).

In general, the adults emerged from the large hosts were larger in size than those emerged from small hosts ($F_{1,73} = 44.80$, $P < 0.001$) and the females were larger than the males ($F_{1,73} = 11.34$, $P < 0.01$). Body size dimorphism was found in males and females emerged from large hosts, but not in those emerged from small hosts (Fig. 2). Asymmetric increase in body size was found in male and female *D. rapae* emerged from small and large hosts. Females emerged from large hosts were on average 13 % larger than females from small hosts ($F_{1,39} = 34.26$; $P < 0.001$) while males from large hosts were 5 % larger than males from small hosts ($F_{1,35} = 12.43$, $P < 0.01$).

Resource/nutrient allocation to male and female *D. rapae*

RAI depended on the size of the host and the sex of the parasitoid developing in host ($F_{3,64} = 83.23$, $P < 0.001$). The mean RAI was greater in smaller hosts than in larger hosts (Fig. 3), indicating that in small hosts, larger proportion of the host resources

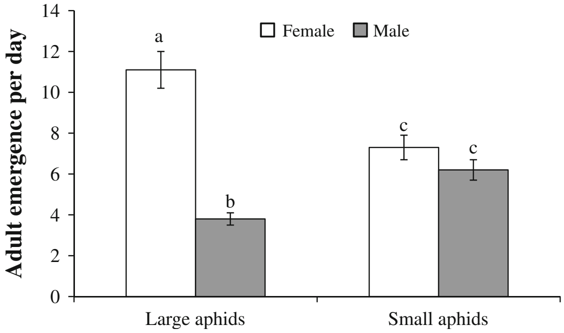

Fig. 1 Mean (±SE) number of male and female *D. rapae* emerged per day from large (5–6 day old) and small (1–2 day old) *B. brassicae* nymphs. Means with the same letters are not significantly different at $\alpha = 0.05$ (Tukey's HSD)

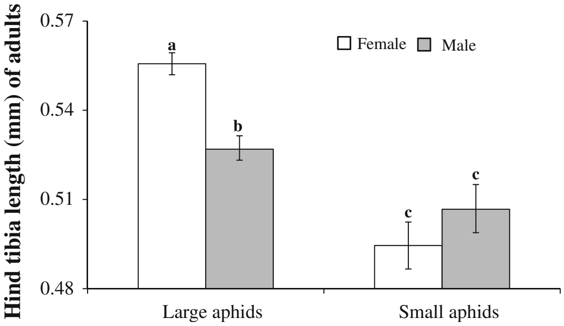

Fig. 2 Mean (±SE) body size (hind tibia length) of male and female *D. rapae* emerged from large (5–6 day old) and small (1–2 day old) *B. brassicae* nymphs. Means with the same letters are not significantly different at $\alpha = 0.05$ (Tukey's HSD)

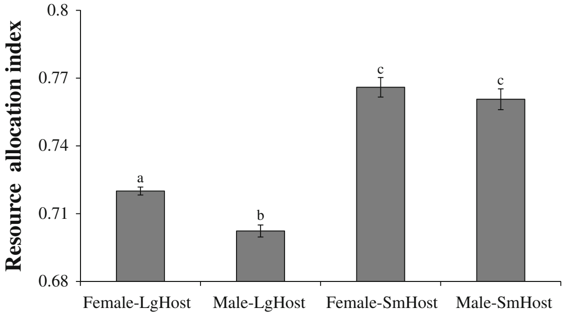

Fig. 3 Mean (±SE) values of Resource allocation index (RAI) for male and female *D. rapae* developed in large (5–6 day old, Lg) and small (1–2 day old, Sm) *B. brassicae* nymphs. Means with the *same letters* are not significantly different at $\alpha = 0.05$ (Tukey's HSD)

Table 1 Mean (±SE) total offspring and female offspring produced from different mating combinations of "large" and "small" male and female *D. rapae*

Mating combination	Total no. of offspring	Female offspring
Large male × large female	66.9 ± 6.4a	46.4 ± 2.4a
Large male × small female	48.1 ± 2.7b	36.7 ± 2.3b
Small male × large female	60 ± 4.2a	35.4 ± 2.4b
Small male × small female	38.7 ± 3.6c	25.3 ± 2.5c

Adults emerged from five to six day old parasitised *B. brassicae* nymphs were considered "large", while adults emerged from one to two day old parasitised nymphs were considered "small". Within a column, means with the same letters are not significantly different at $\alpha = 0.05$ (Tukey's HSD)

were allocated to developing parasitoids. There was no significant difference in RAI of males and females developing in smaller hosts. RAI of females developing in larger hosts was greater than RAI of males developing in those hosts (Fig. 3).

Reproductive gain in large and small *D. rapae*

The number of offspring produced by *D. rapae* depended on the body size of male and female parasitoids ($F_{3,51} = 14.37$, $P < 0.001$). The mean (±SE) number of offspring produced by larger females (63.7 ± 2.3) was significantly greater than the number of offspring produced by smaller females (43.9 ± 2.4) (Table 1). The number of offspring produced by a large female mated with a large male was significant greater than the number of offspring produced by a large female mated with a small male. However, the number of offspring produced by small females was similar whether they mated with large or small males (Table 1). Mating combination "large male × large female" produced the highest number of females (Table 1). When the sex ratios of the offspring produced by small and large males were compared, larger males produced a higher proportion of females (logistic regression: $\chi^2 = 12.25$, df = 1, $P < 0.001$).

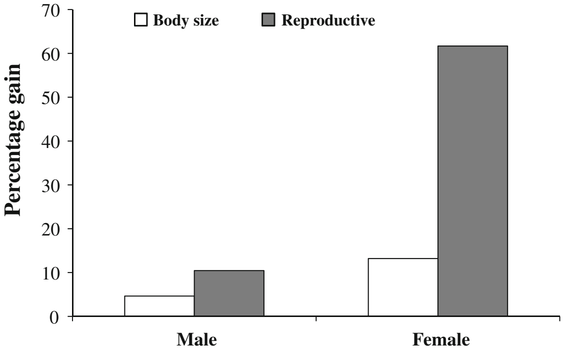

Fig. 4 Body size gain and reproductive fitness gain in male and female *D. rapae* developed in large (5–6 day old) *B. brassicae* nymphs, % increase relative to individuals developed in small (1–2 day old) aphid nymphs. Fitness gain in males was calculated in terms of increase in female progeny while fitness gain in females was calculated in terms of total (combined male and female) progeny

Body size gain *versus* reproductive fitness gain

An asymmetry was observed between body size gain and reproductive fitness gain in male and female *D. rapae*. Although both male and female *D. rapae* gained body size by developing in larger hosts, the females gained disproportionately more fitness than males by developing in larger hosts (Fig. 4).

Discussion

Growth of *D. rapae* larvae developing inside aphid nymphs was affected by the size of nymph in which oviposition occurred. The parasitoid larvae have finite resources for completing their development, limited to whatever is available in a single host (Godfray 1994). The large body size of larvae developing in the larger hosts suggests that large hosts contained more resources that were immediately available to the newly hatched larvae, compared to the smaller hosts.

Studies of superparasitism in *D. rapae* suggested that more resources are available in larger hosts because 2–5 parasitoid larvae can develop simultaneously without compromising their growth, although only one individual completes its development (Kant et al. 2011; Kant et al. 2012a). The smaller cabbage aphid nymphs did not sustain development of more than two larvae per host, and higher host mortality was found in small superparasitised aphids (Kant et al. 2011).

Emergence of larger adults from larger hosts further suggests that more of resources are available in larger hosts. Larger hosts also provide more space to the developing parasitoid larva while larvae developing in small hosts have limited space for growth before host mummification. The size of males and females that developed in small hosts was similar, but a clear sexual dimorphism was found between those developed in large hosts, with females significantly larger than males. Females emerged from larger hosts were significantly larger than those emerged from small hosts, while the increase in body size of males was not significant. This suggests that resources available in small hosts are sufficient for males to attain a maximum body size, but might be limiting for females.

Sexual dimorphism has also been found in a wild population of *D. rapae* (Kant et al. 2012b). The evolutionary consequences in fitness gain are expressed as foraging behaviour of *D. rapae* females, which prefer to allocate fertilised (female) eggs to larger hosts (Charnov et al. 1981). Solitary parasitoids developing in larger hosts will benefit in terms of increased adult size which is predicted to be positively correlated with life-history and demographic characters such as fecundity and survival (Mackauer and Sequeira 1993; Kant et al. 2012a).

Diaeretiella rapae is a koinobiont species, which allows its host to develop and reproduce (Zhang and Hassan 2003). Some of the resources acquired by the parasitised aphid hosts for their own growth and reproduction are sequestered to the growth of parasitoid larvae. Couchman and King (1979) found that the feeding rate of parasitised cabbage aphids varied in relation to the growth and development of *D. rapae* larvae in the aphid body. The resources available in hosts (especially small hosts) at the time of oviposition are not sufficient for the parasitoids to complete their development. Rather, their development depends on the host continuing to feed and grow (Sequeira and Mackauer 1992). In smaller hosts, due to lower feeding efficiency, the parasitoid might lack resources and as a result consume the aphid nymphs developing simultaneously with the parasitoid in the parasitised host. In this study, when large parasitized aphids were dissected after four days of parasitism they contained parasitoid larvae and underdeveloped aphid nymphs, whereas only parasitoid larvae were found inside the body of small parasitised aphids. Larger hosts might have enough resources at the time of oviposition for parasitoids to complete their development, although hosts have to survive long enough (Godfray 1994).

The total number of offspring and the progeny sex ratio of *D. rapae* were affected by the body size of both parents, indicating that both sexes contribute to the fitness of *D. rapae*. Larger *D. rapae* females emerge with higher egg load (Kant et al. 2012a) and produce more offspring than smaller females (Chown and Gaston 2010). Females mated with larger males produced significantly more female offspring, suggesting that the body size of the male *D. rapae* has a strong influence on the progeny sex ratio. This could be due to higher sperm stock of males emerged from larger hosts (Lacoume et al. 2006). The progeny sex ratio was not significantly different between "large male × large female" and "small male × small female" combinations, suggesting that females can manipulate the number and proportion of female progeny to maintain the male/female balance in the population.

A large number of reproductive behaviours of parasitoids are influenced by their body size, which affects their fitness (Stearns 1992; Sagarra et al. 2001). Greater longevity of large female *D. rapae* allows them to reproduce longer (Kant et al. 2012a). Large *D. rapae* males may be able to inseminate more females, as has been shown for larger males of *Dinarmus basalis* (Lacoume et al. 2006). Furthermore, large males and females benefit during intersexual mate selection (Visser 1994; Joyce et al. 2009). Larger males have been found to win the male–male combats during mating, which are common in hymenopterans (Abe et al. 2005; Joyce et al. 2009). Female *D. rapae* might gain fitness by producing larger males in the presence of conspecific competition, where larger males have the advantage over smaller ones in male–male combat.

The results indicate that larger hosts immediately provide more resources to the developing parasitoid larvae. Resources gained by *D. rapae* larvae affected their body size and their reproductive fitness. Larger males and females produced more progeny as well as a higher proportion of females. The increase in body size and the gain in reproductive fitness were not symmetrical in male and female *D. rapae*. Females received disproportionately more benefit than males by developing in larger hosts.

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