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## Biocontrol Science and Technology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/cbst20>

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Accepted author version posted online: 03 Nov 2011. Version of record first published: 20 Jan 2012

To cite this article: R. Kant, M.A. Minor & S.A. Trewick (2012): Reproductive strategies of *Diaeretiella rapae* (Hymenoptera: Aphidiinae) during fluctuating temperatures of spring season in New Zealand, *Biocontrol Science and Technology*, 22:1, 1-9

To link to this article: <http://dx.doi.org/10.1080/09583157.2011.635248>

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## Reproductive strategies of *Diaeretiella rapae* (Hymenoptera: Aphidiinae) during fluctuating temperatures of spring season in New Zealand

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*(Received 21 July 2011; returned 30 September 2011; accepted 21 October 2011)*

Reproductive activities of naturally occurring population of *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Aphidiinae) on *Myzus persicae* were studied during spring season in New Zealand. The cabbage seedlings were highly infested with the aphids ( $272 \pm 25$  individuals/plant) with about 30% on average parasitised by *D. rapae*. Rate of parasitism was positively correlated with the aphid density ( $R^2 = 0.64$ ). Adult emergence from aphid mummies was 90%, with a higher frequency of females than males. Increase in female/male sex ratio was found between early and late spring (1.1 vs. 1.8). Mating in *D. rapae* occurred throughout the day. Nearly half of the mating pairs collected were male–male pairs, which were especially prevalent during morning and evening while more male–female mating pairs were found during midday. Male–male mounting was probably because of low number of virgin females in morning and evening populations. About 80% females were mounted by smaller size males. Male–male mounting is discussed in correlation with operational sex ratio of *D. rapae* population.

**Keywords:** mating; sex ratio; male-male mounting; ambient environment; *Diaeretiella rapae*

### Introduction

Aphids are significant and cosmopolitan agricultural and horticultural pests. In New Zealand, aphids cause substantial economic loss to the agricultural industry and it is predicted that global climate change will further aggravate the aphid problem (Gerard et al. 2010). The common method for controlling aphids is application of chemical pesticides, but the indiscriminate nature of these agents causes various problems, including evolution of insecticide resistance in aphids (Clark and Yamaguchi 2002), and toxicity to their natural enemies (Desneux, Decourtye, and Delpuech 2007). In New Zealand, pesticides are widely used, but there is a trend toward alternative options of Integrated Pest Management (IPM) and biological control methods (Manktelow et al. 2005). *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Aphidiinae) is a solitary endoparasitoid of more than 60 different aphid species worldwide (Pike et al. 1999). The wasp originates from the Western Palaearctic, but is now distributed throughout the world, and was accidentally introduced to New Zealand, where it has established (Carver and Starý 1974). Among the common

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hosts of *D. rapae* in New Zealand and other countries are cabbage aphid, green peach aphid, and lettuce aphid (Mackauer and Starý 1967; Carver and Starý 1974; Kavallieratos et al. 2001, 2005). In the USA, *D. rapae* has been used in biological control of Russian wheat aphid (Bernal 1993). In Australia it was deliberately introduced for controlling cabbage aphid (Carver and Starý 1974). Little attention has been given to *D. rapae* as a potential biological control agent of aphids in New Zealand, probably because *D. rapae* is not well studied here.

Unlike predators, the pest suppression ability of a parasitoid is directly linked to its reproductive strategy. Mating and oviposition behaviours are the two main aspects that affect the reproductive performance of parasitoids. Importantly, the reproductive potential of parasitoids is environmentally sensitive and it changes with climatic and geographical location (Jervis, Ellers, and Harvey 2008). Climatic conditions, including temperature and day length, strongly influence biological traits such as host searching, oviposition, sex allocation, immature development, adult emergence, and mating, which further affects the host–parasitoid system in nature (Legrand, Colinet, Vernon, and Hance 2004). Rakhshani et al. (2008) showed the effect of altitude (and, therefore, temperature) on aphid parasitoids. For example, *D. rapae* and *Aphidius rhopalosiphi* De Stefani (Hymenoptera: Braconidae: Aphidiinae) parasitized cereal aphids at high altitudes, while *Ephedrus persicae* Froffat (Hymenoptera: Braconidae: Aphidiinae) and *Ephedrus plagiator* Nees (Hymenoptera: Braconidae: Aphidiinae) preferred lower altitude.

Studying reproductive behaviour of a local population will improve understanding of the reproductive strategies of *D. rapae*, which is essential for testing its suitability and efficiency in a biological control programme at a local level (Lewis, Vet, Tumlinson, van Lenteren, and Papaj 1990). The current study investigated parasitism and mating activities for a wild New Zealand population of *D. rapae* at ambient conditions during the fluctuating weather of the spring season (September to December). The study sought to (1) assess parasitism patterns of *D. rapae*, (2) determine sex ratio changes of *D. rapae* over time and in relation to parasitism rate, and (3) reveal the scale of sexual dimorphism and its effect on mating attempts in *D. rapae* adults.

## Materials and methods

Parasitism and mating activities of *D. rapae* were studied in a 25-m<sup>2</sup> shade-house in an open/ambient environment from September to December 2009 in Palmerston North, New Zealand. Weather conditions in New Zealand during the spring are typically variable and we recorded temperature and humidity during the study period (Table 1). The area contained approximately 544 potted cabbage seedlings (cv. ‘Summer globe’) aged 2–4 months, which were regularly irrigated with an automatic watering system (Temporizador T 14 e, Gardena AG, Germany). The temperature, humidity and day length conditions were ambient. Green peach aphid *Myzus persicae* and its parasitoid *D. rapae* colonised the area naturally, and were left undisturbed for 3 months prior to taking observations. The parasitoid was identified according to Powell (1982) and corroborated by comparison of mtDNA sequences with published data (Baker, Loxdale, and Edwards 2003).

Table 1. Mean average weekly temperature and humidity during the eleven week study period, Palmerston North, New Zealand. Source: The National Climate Database, NIWA, Wellington.

Week No.	Week of	Mean Temp °C	Relative humidity (%)
1	21-Sep	8.8	80.61
2	28-Sep	11.9	85.39
3	5-Oct	7.5	78.37
4	12-Oct	12.1	84.56
5	19-Oct	8.6	78.67
6	26-Oct	9.7	78.24
7	2-Nov	12.3	80.13
8	9-Nov	10.3	77.23
9	16-Nov	13.5	80.15
10	23-Nov	13.8	81.92
11	30-Nov	14.7	82.85

### ***Parasitism rate, sex ratio and size dimorphism in D. rapae***

Aphid infestation and parasitism were recorded at weekly intervals for an 11-week period starting from 21 September 2009. Each week, two infested plants were chosen at random, and the number of parasitised and unparasitised aphids on upper and lower leaves of the plants was recorded. The parasitized aphids (mummies) were transferred into individual 2-mL microfuge tubes using a fine paint brush. The mummies were regularly monitored and the adults were sexed using a stereomicroscope (Olympus SZX12) as they emerged. The size of the males and females was measured for estimating the body size dimorphism in male and female *D. rapae*. The hind tibia length was measured as proxy for body size, as our earlier studies found them to be highly correlated ( $R^2 = 83.56$ ,  $P < 0.001$ ) (R. Kant, unpublished data). The adults were killed by freezing at  $-20^\circ\text{C}$  and then stored in 70% ethanol until measuring. The hind tibia was dissected from the thorax of the insect on a glass slide in saline, and measured using calibrated eyepiece micrometer.

### ***Mating pairs of D. rapae***

To understand the relationship between the body size of mating male and female *D. rapae*, all pairs observed in the area during the 1-h search were collected using a hand-held aspirator made from a 10-mL glass vial. Mating activities of the parasitoids were observed, and mating pairs of *D. rapae* were collected once every 3 days at three times of the day: 7–8 am (morning), 12–1 pm (midday), and 5–6 pm (evening). The body size and sex of the pairs attempting to copulate were determined.

### ***Statistical analyses***

A goodness-of-fit test was performed to assess the normality of data before analyses and, when required, non-normal data were transformed prior to analysis. Body sizes of males and females, and the sex ratio in the first and last 5 weeks were subjected to analysis of variance (ANOVA). Regression analysis was applied to examine the relationship between aphid density and parasitism rate, the trend in the sex ratio of

parasitoids, and the relationship between body sizes of male and female mates. A chi-squared test was used to determine the difference in the number of male–female and male–male mating observed at different times of the day. Analyses were carried out using SAS Enterprise Guide 4.2. Significance level set to the analyses was  $P = 0.05$ .

## Results

### *Parasitism rate, sex ratio and size dimorphism in D. rapae*

The cabbage seedlings were heavily infested with aphids and parasitoids. The mean numbers ( $\pm$ SE) of live aphids and parasitised mummies were  $272 \pm 25$  and  $71 \pm 7$  per plant, respectively. Most aphids (95%) and aphid mummies (91%) were recovered from undersides of cabbage leaves. The parasitism rate fluctuated between 23 and 39% during the study period (Figure 1) and no specific trend in parasitism rate during the 11-week study period was found ( $P = 0.53$ ). The mean number ( $\pm$ SE) of aphids parasitised during the first 5 weeks ( $94 \pm 10$ ) was less than the number of aphids parasitised during the second 5-week period ( $131 \pm 18$ ) ( $P = 0.023$ ). The number of mummies recovered from infested plants was directly correlated with the density of the aphids on the plant ( $P < 0.001$ ) (Figure 2).

The rate of parasitoid emergence from mummies was very high ( $92 \pm 6\%$ ), with the number of emerging females greater than the number of males during the entire study period. The proportion of female offspring increased from the beginning to the end of the study period (Figure 3). The mean female/male ratio of emerging parasitoids was significantly higher during the second 5 weeks of the study ( $1.6 \pm 0.1$  5-week average) compared to the first 5-week period ( $1.2 \pm 0.1$ ) ( $P < 0.05$ ).

The body size of male and female *D. rapae* ranged widely; the hind tibia length of males ranged 433–601  $\mu\text{m}$  and that of females 408–622  $\mu\text{m}$ . The mean hind tibia length of males was significantly smaller than the females ( $P < 0.001$ ) (Figure 4).

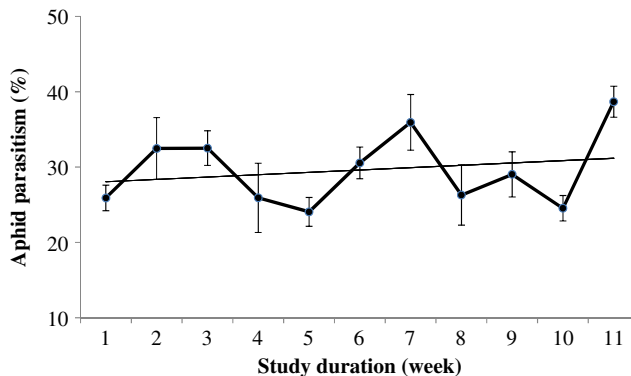


Figure 1. The mean ( $\pm$ SE) percentage parasitism of *Brevicoryne brassicae* nymphs parasitised by *Diaeretiella rapae* during eleven week period (3rd week of September to 1st week of December 2009).

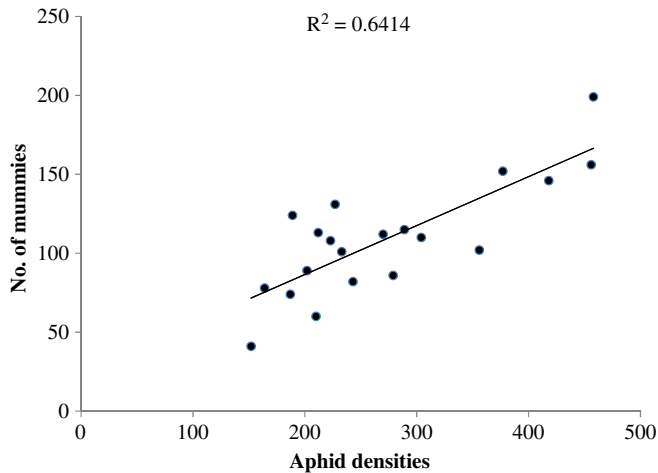


Figure 2. Relationship between aphid density and number of aphid mummies recovered per plant (parasitism rate).

**Mating pairs of *D. rapae***

Overall, 49% of the mating pairs comprised a male mounted on a female and 45% were male mounted on another male. There were few instances of female–female pairs (1%) and female–male–male mounting (5%).

When the mating pairs were partitioned by the time of day, it was found that male–female mating was more prevalent during midday compared to morning and evening ( $\chi^2 = 8.89$ ;  $P < 0.05$ ). About half of the mating pairs were male–female during morning (48%) and evening (46%) (Table 2).

Most females (79%) in male–female mating pairs were found to be mounted by males with body size smaller than themselves, with males on average 16% smaller than their female partners (Figure 5) ( $P < 0.005$ ). There was no significant difference in body size of males in male–male pairs ( $F_{1, 40} = 0.14$ ,  $P = 0.711$ ).

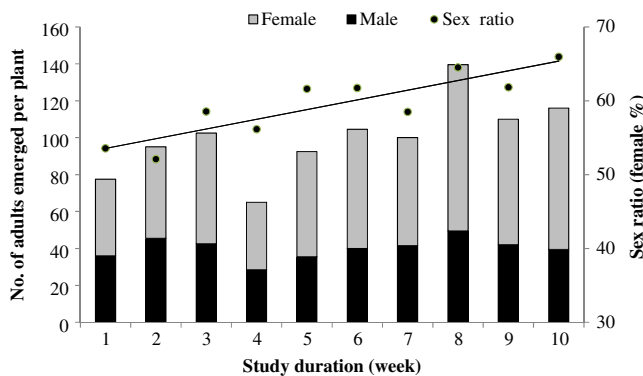


Figure 3. Mean number and the sex ratio (female%) of emerging *Diaeretiella rapae* (per plant) during ten week period, beginning from 21<sup>st</sup> September 2009.

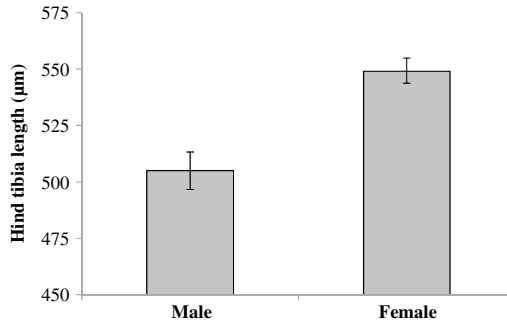


Figure 4. The mean ( $\pm$ SE) body size (as hind tibia length) of male and female *Diaeretiella rapae* emerged from parasitised mummies.

### Discussion

The low rate of parasitism during the first 5 weeks of the experiment indicates low reproductive output of *D. rapae* during lower temperatures of spring. Temperature threshold and thermal constants for parasitoid activities are usually higher than those for their hosts (Campbell, Frazer, Gilbert, Gutierrez, and Mackauer 1974). After winter, the aphid population can grow quickly during the early season due to their low temperature threshold, whereas *D. rapae* take longer to develop at low temperatures (Shukla, Prasad, and Singh 2008), resulting in poor synchronisation between parasitoid and aphid populations (Liu 1989). Kavallieratos, Athanassiou, Stathas, and Tomanovi (2002) found that, for this reason, Aphidiinae parasitoids could not suppress the aphids infesting citrus during spring and early summer. Zhang and Hassan (2003), and Fathipour, Hosseini, Talebi, and Moharramipour (2006) suggested that the low parasitoid/host ratio during the spring season adversely affects the efficiency of *D. rapae* in suppressing the aphid population. In our study, a slight increase in the *D. rapae* parasitism rate of *B. brassicae* was observed towards the end of spring, suggesting an increase in parasitoid/host ratio. This can be explained by increase of the mean air temperature in the late spring. According to Hayakawa, Grafius, and Stehr (1990) high temperatures ( $>30^{\circ}\text{C}$ ) increased the fecundity and daily oviposition of *D. rapae* parasitising *Brachycorynella asparagi* Morvilko (Hemiptera: Aphididae) on asparagus.

In haplodiploid parasitoids, a female-biased sex ratio can facilitate rapid population increase (Godfray 1994). Although males are essential for the production of female offspring in *D. rapae*, their number does not need to be on a par with females, because males can mate up to six times, while females are monandrous (Kant

Table 2. Total number of mating pairs of *Diaeretiella rapae* captured in the morning (7–8 am), at midday (12–1 pm) and in the evening (5–6 pm). Within each column, the same letter indicates no significant difference ( $P > 0.05$ ).

Mating pairs	Morning	Midday	Evening
Male x Male	26 a	20 a	48 a
Female x Male	24 a	39 b	41 a
Total mating pairs	50	59	89

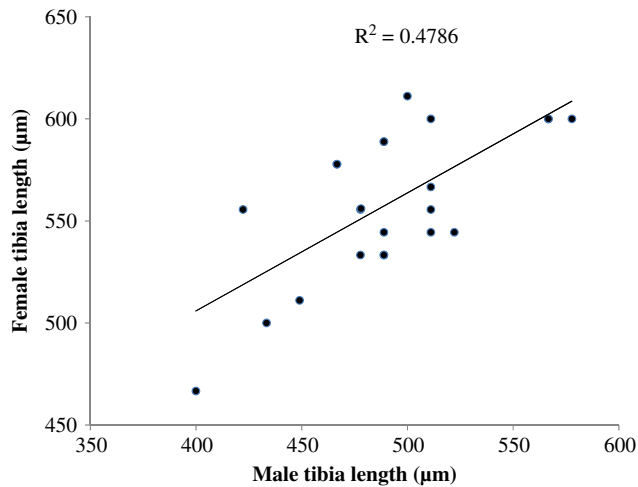


Figure 5. Relationship between body sizes (as hind tibia length) of male and female in *Diaeretiella rapae* mating pairs.

2009). Unmated females produce only male offspring. If a female remains unmated or mating is delayed, the parasitoid population in subsequent generation will be even more male-biased, which affects the parasitoid ability to suppress the host population. Thus, an increase in female/male sex ratio is a primary requirement for *D. rapae* to provide better aphid suppression. The pattern of change in sex ratio found in this study suggests higher parasitoid/aphid ratios in late spring, and thus better suppression of the aphid population is more likely to be achieved in summer.

High numbers of males in the population could negatively influence the mating system. Among the pairs of *D. rapae* attempting copulation, only 49% were male–female pairs. The high number of erroneous male–male attempted copulations could not be explained by males ‘misinterpreting’ the sex of larger individuals as females, as no size difference was found in male–male pairs. We think that male–male copulatory attempts may represent the intrasexual aggressive behaviour of males competing for mates, which has been found in other hymenopteran species (Al-Wahaibi, Owen, and Morse 2005)

Higher percentage of male–female matings during the midday indicates that more virgin females were available in the population during the midday, compared to morning and evening. Diurnal emergence patterns of *D. rapae* showed that males emerge prior to females, and the majority of males emerge during the first few hours of the morning (Kant and Sandanayaka 2009). Moreover, the males surviving from previous days further add to the male numbers in the morning population. Thus, morning populations may have overabundance of males and be female-limited. The majority of females emerge by the middle of the day (Kant and Sandanayaka 2009), and by late afternoon/evening most of the newly emerged virgin females would have been mated, which leads to another shortage of females observed in the evening.

In an open system, where hundreds of males and females of different sizes are available simultaneously, a female may show its preference for a particular size of male for mating. Although males are aggressive during mating, the mating success largely depends on a female; they mate only once during their entire life so must choose a good



quality male to maximise reproductive fitness. The quality of males can be inferred from their body size (Godfray 1994) which differs between males and females in *D. rapae* (Kant, Minor, and Trewick 2011). Our results suggest better mating success or mating compatibility in *D. rapae* when males are slightly smaller than females.

During the relative unstable spring weather conditions of September to November in New Zealand, the aphid population increases rapidly due to parthenogenetic reproduction. We have found that periods of colder weather in New Zealand slow the generation time of *D. rapae* and thus contribute to a low parasitism rate early in the season, when the aphid population is already high. *D. rapae* cannot respond by using parthenogeny, as this generates males that have no parasitic capacity. Excess number of male wasps reduces parasitism rate and also mating rate, and thus drives low female/male ratio in early spring. For biological control to be effective, pre-release of *D. rapae* for suppression of early population-explosion of the aphid host is required (Godfray 1994). Therefore, careful consideration should be given to the measurement and management of sex ratio in wild and captive reared populations. These results highlight the need for more detailed study on mating and oviposition behaviour of *D. rapae* in New Zealand to optimise their performance in aphid suppression.

### Acknowledgements

The research is supported by a Massey University Doctoral Research Scholarship. We are thankful to Mr Diwas Khatri for his help in growing cabbage seedlings.

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