



## Effects of mating and oviposition delay on parasitism rate and sex allocation behaviour of *Diaeretiella rapae* (Hymenoptera: Aphidiidae)

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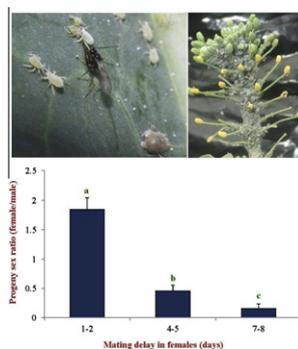
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### HIGHLIGHTS

- ▶ Female *Diaeretiella rapae* emerge with developed eggs.
- ▶ Oviposition delay resulted in decreased parasitism by *D. rapae*.
- ▶ Delay in mating did not affect courting but affected the reproductive capacity of male and female *D. rapae*.
- ▶ Mating delay caused overproduction of male *D. rapae*.
- ▶ One-two day old *D. rapae* adults could perform more efficiently than younger or older adults as biocontrol agents.

### GRAPHICAL ABSTRACT



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### ABSTRACT

Mating and oviposition complement each other in parasitoid reproduction; delay in either of these activities has disparate consequences for the fitness of the parasitoid. We investigated the effects of mating and oviposition delay on parasitism rate and progeny sex ratio in a parasitic wasp *Diaeretiella rapae*. Egg dynamics in the ovaries of females of different ages, and females which completed different numbers of oviposition bouts were also examined. Delay in mating and oviposition adversely affected reproductive performance of both male and female *D. rapae*. Delayed oviposition resulted in reduced parasitism rates in both mated and unmated females. The progeny sex ratio was female-biased, but the proportion of female offspring decreased towards the end of *D. rapae* life. Although females emerged with developed eggs, the egg load in the ovaries of unmated and naïve females initially increased then continuously decreased with age, suggesting partial resorption of eggs towards the end of a females life. Oviposition rate of unmated females was low before mating. The extent of mating delay experienced by females affected the sex ratio of their progeny, causing overproduction of males. Delayed mating did not affect the courting capacity of males, but reduced the number of their offspring and proportion of female offspring. The duration of copulation was longer in older males. The results of this study clearly indicate the importance of parasitoid age in biological control programmes, and suggests the use of 1–2 days old *D. rapae* for best results.

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### 1. Introduction

Mating and oviposition are two essential activities in sexually-reproducing insects. In parasitoids, reproductive efficiency is

directly linked to their ability to suppress the pest population. For example, in solitary parasitoids where females oviposit one egg per host, fecundity is generally equivalent to the expected number of hosts killed by the parasitoid unless females superparasitise, laying more than one egg per host. Although the two activities – mating and oviposition – complement each other in reproduction of parasitoids, their timing and sequence can affect

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reproductive fitness (Damiens et al., 2003; Fauvergue et al., 2008; Kant et al., 2012c). Oviposition or mating could be delayed when hosts or mates, respectively, are limited.

When female parasitoids emerge, they have a choice between oviposition and mating (Godfray, 1994; Kant et al., 2012c). Females can oviposit before or without mating, but pre-mating oviposition in arrhenotokous parasitoids will result in haploid male progeny and could imbalance the sex ratio of the population in the next generation (King, 1962). Mating is required for producing fertilised eggs which result in female offspring (Godfray, 1994). Mating is, therefore, an essential component of parasitoid fitness in terms of the ability of parasitoids to carry on their generation, and for maintaining the sex ratio of the population (Hardy et al., 2007). High sex ratio (female/male) is always desirable for effective biological control of insect pests, because females are directly responsible for reducing the pest population (Kant et al., 2012b; Ode and Hardy, 2008).

The number of eggs a female parasitoid carries is an indicator of its reproductive output (Godfray, 1994). In pro-ovigenic parasitoid species, females emerge with all their potential eggs ready to be oviposited, while in synovigenic parasitoids females emerge with immature eggs and can produce new eggs throughout their adult life (Flanders, 1950). Females of these two types of parasitoids may face disparate consequences of oviposition delay (Jervis et al., 2001) – synovigenic females can regulate their egg load by resorbing and replenishing eggs depending upon the availability of hosts, but if a pro-ovigenic female reabsorbs her eggs, the eggs may not be replenished. Parasitoids are time-limited and also egg-limited if they are pro-ovigenic or weakly synovigenic. When females emerge with mature eggs, even a short delay in oviposition could reduce their reproductive potential. Females also reabsorb their eggs in the absence of hosts (Guo et al., 2011; Richard and Casas, 2009), and this resorption could adversely affect their reproductive potential. Earlier studies showed that while the temporary host deprivation in proovigenic *Trichogramma* sp. did not affect the overall progeny production or sex ratio (Fleury and Bouletreau, 1993), the reproductive potential of parasitic wasp *Microplitis rufiventris* was affected when they were host-deprived (Hegazi et al., 2007).

Here we examined the effects of mating and oviposition delay on reproductive fitness of *Diaeretiella rapae* (McIntosh) (Hymenoptera: Aphidiidae) which could undermine the use of *D. rapae* or other parasitoids in biological control. A little information is available on oviposition or mating delay in *D. rapae* or other Aphidiidae. *Diaeretiella rapae* is a solitary endoparasitoid of more than 60 aphid species (Homoptera: Aphididae) infesting cruciferous and non-cruciferous plants (Pike et al., 1999) and it is the only recorded parasitoid of the cabbage aphid *Brevicoryne brassicae* (George, 1957). Cabbage aphid is an important agricultural pest, causing severe damage to crops in many countries including New Zealand (Hughes, 1963; Lammerin and Morice, 1970).

Female *D. rapae* live longer than males, and their longevity depends on their body size (Kant et al., 2012a) and food. The ovigeny status of *D. rapae* is not clear. Bernal et al. (1997) suggested *D. rapae* is a pro-ovigenic species as females emerge with abundant developed eggs and reproduce most of their progeny during the first half of their life. However, another study suggested that *D. rapae* is a synovigenic species (Tyllianakis et al., 2004). Male *D. rapae* emerge earlier than females (Kant and Sandanayaka, 2009), which increases the probability of females being mated quickly upon emergence. Female *D. rapae* prefer to oviposit after mating (Kant et al., 2012c). However, even if the females are mated upon emergence, they may not find suitable hosts for parasitism. Therefore, understanding the impact of mating and/or oviposition delay on the efficiency of *D. rapae* can be useful during mass production and release of parasitoids in biological control programmes. This study sought to (1)

assess the effects of oviposition delay on parasitism rate in mated and unmated female *D. rapae*; (2) examine the effect of adult age on egg-count in *D. rapae* and (3) investigate the effect of delayed mating in male and female *D. rapae* on the progeny sex ratio.

## 2. Materials and methods

### 2.1. Insect cultures

Colonies of *D. rapae* and cabbage aphid were established in the laboratory from insects collected in a cauliflower field in Palmerston North, New Zealand, and maintained in a controlled environment at  $20 \pm 2$  °C,  $65 \pm 10\%$  RH and 16 h photoperiod. The same environmental conditions were used for all experiments. Cabbage aphid nymphs of preferred age and size (5–6 days old) were used in the experiments. All parasitoids used in the experiments were fed with 10% honey solution after emergence.

### 2.2. Oviposition delay in unmated females

Most *D. rapae* emerge during early to mid photophase (Kant and Sandanayaka, 2009). The first oviposition in newly emerged females (2–4 h old) was recorded on the day of emergence. Newly emerged unmated female *D. rapae* ( $n = 10$ ) were individually exposed to 60 cabbage aphid nymphs per day on a cabbage seedling for 3 consecutive days. The parasitised aphids were allowed to feed and develop on the seedling. Once the aphids were mummified, they were transferred to individual 2 ml microfuge tubes. The mummies were observed daily for adult emergence. To understand the effect of oviposition delay on parasitism, similar experiments were performed with unmated females 1, 3 and 6 days old that had not been exposed to aphids since emergence. The number of offspring that emerged from each age group was compared with the number of offspring produced by newly emerged females. Each age group was replicated 10 times.

In a separate test, the egg-loads of newly emerged (2–4 h old) female *D. rapae* and females of age 1–2, 3–4, 7–8 and 9–10 days, that had not been exposed to aphid hosts, were examined under a stereomicroscope (Olympus SZX12). Ovaries were excised from the abdomen of each female on a glass slide in saline solution, and a cover slip was placed gently on the ovaries. Pressure on the cover slip made the ovaries burst so the eggs could be counted. In each age group 10–15 females were dissected.

### 2.3. Oviposition delay in mated females

Newly emerged female *D. rapae* were each paired with a 1-d old virgin male and their mating observed. Each mated female ( $n = 10$ ) was offered 60 cabbage aphid nymphs per day on a cabbage seedling for 3 consecutive days. The same experimental protocol from oviposition until adult emergence was followed as in the unmated females experiment. The parasitism rate and progeny sex ratio of three female age groups (1, 3 and 6 days old) mated but not exposed to aphids were compared with those of newly emerged females (2–4 h old). Each female age group was replicated 10 times.

### 2.4. Mating delay in males and females

To test whether newly emerged male *D. rapae* are able to mate and transfer sperm during mating, males less than 1 h old ( $n = 10$ ) were individually paired with 1-day old virgin females. Females that did not mate within 30 min were discarded. Mated females were then provided with honey for 6 h before being offered 15 aphids per female for parasitism. After mating, female insects generally store sperm in their spermatheca before fertilising their eggs

(Quicke, 1997). In several species female cannot use sperm immediately after copulation, and the period between mating and fertilization can vary considerably in parasitoids (Hardy et al., 2007). Our earlier study indicated that a female needs at least 6 h to fertilise her eggs. Therefore, females were held for 6 h to ensure that they had sufficient time to fertilise their eggs and produce female offspring. The number and sex of the offspring that emerged from parasitised aphids were recorded.

Similarly, the parasitism rate and sex ratio of offspring produced by the females mated with virgin males of different ages (1–2 days, 4–5 days and 7–8 days old) were investigated. Individual virgin males in each age-group were offered two 1-day old virgin females together for 24 h. This allowed each male to mate with one or both of the available females and it is known that sperm depletion occurs in *D. rapae* only after three or more matings (Kant et al., 2012d). Each of the mated females was then offered 15 unparasitised aphids per day for 3 consecutive days. The number of female offspring produced by the females mated with males of each age group was compared. The number of female offspring produced was used as an indirect estimate of sperm transfer (Godfray, 1994; Henter, 2004). More than ten males were tested in each male age group treatment.

The effects of different periods of mating delay (1–2 days, 4–5 days and 7–8 days) on parasitism rate and sex ratio of the female's offspring were tested. All females were offered 15 aphids for parasitism from the first day of emergence. Since haplodiploid females can reproduce before mating, offering hosts before mating likely to reflect natural conditions, and helps reveal the pre-mating and post-mating oviposition strategies of female *D. rapae*. When the females reached the desired mating age for the experiment, they were each paired with a 1-day old virgin male for 24 h. After mating, each female was again offered 15 aphids per day for three consecutive days, irrespective of the mating delay period. This means that in 1–2 day delay treatment, the females mated prior to first oviposition, while the group of females which were not exposed to males for the first four days of their emergence already oviposited for 3 days prior to mating; similarly, the group of females which were not exposed to males for the first 7–8 days of their emergence, oviposited for 6–7 days prior to mating. Each treatment was replicated 10 times. The total number of offspring and the proportion of female produced by each group of females were compared.

### 2.5. Statistical analysis

A goodness-of-fit test was used to assess the distribution of the data, and the non-normal data were transformed prior to analyses. The number of offspring produced by mated and unmated females in oviposition and mating delay experiments, and the number of eggs found in the ovaries of females of different age were analysed using analysis of variance (PROC GLM, SAS 9.2). The means of different treatments were compared using a Tukey's studentised range (HSD) test. Linear regression analysis (PROC REG) was used to examine the relationship between oviposition delay and the number of offspring produced by the females. Logistic regression with binary response variable (PROC LOGISTIC, SAS 9.2) was used to analyse the offspring sex ratio in different treatments. Values in results are untransformed means  $\pm$  SE. All analyses were carried out at  $\alpha = 0.05$  level of significance.

## 3. Results

### 3.1. Oviposition delay in unmated females

The number of offspring produced by female *D. rapae* was negatively affected by the duration of oviposition delay (number of

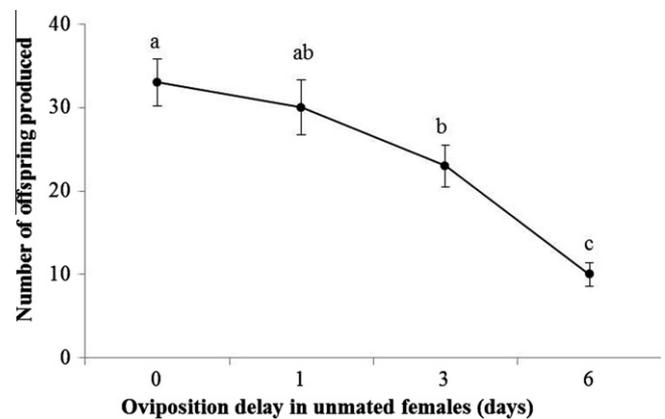


Fig. 1. Total number of offspring (mean  $\pm$  SE) produced by unmated *Diaeretiella rapae* females which were prevented from ovipositing for different periods after their emergence. Means with the same letter are not significantly different at  $\alpha = 0.05$  (Tukey's HSD).

offspring produced =  $41.03 - 4.49x$ , where  $x$  = delay in number of days,  $R^2 = 0.48$ ,  $P < 0.001$ ). Unmated females that were not allowed to oviposit for 6 days, produced less than a third of the total number of offspring they would have produced if their oviposition started soon after emergence ( $F_{3,36} = 11.31$ ,  $P < 0.001$ ) (Fig. 1). There was no significant reduction in the number of offspring produced by females whose oviposition was delayed for a single day.

The egg count in the ovaries of unmated and naïve female *D. rapae* changed with age (Fig. 2). Although females emerged with developed eggs, their egg count initially increased with age, reaching a maximum 3–4 days after emergence, before decreasing ( $F_{4,63} = 62.23$ ,  $P < 0.001$ ) (Fig. 2).

### 3.2. Oviposition delay in mated females

Mated female *D. rapae* that were prevented from ovipositing for the longest period (6 days) produced the least offspring ( $F_{3,36} = 30.99$ ,  $P < 0.001$ ) (Fig. 3). Mated females whose oviposition was delayed for 6 days also produced the least female offspring ( $7.7 \pm 0.63$ ) compared to other mated females ( $F_{3,72} = 20.83$ ,  $P < 0.001$ ) (Table 1). The progeny sex ratio (female-to-male) declined significantly when *D. rapae* oviposition was delayed for 6 days, but not until 3 days delay (Logistic regression:  $\chi^2 = 4.71$ ,  $P < 0.05$ ) (Table 1).

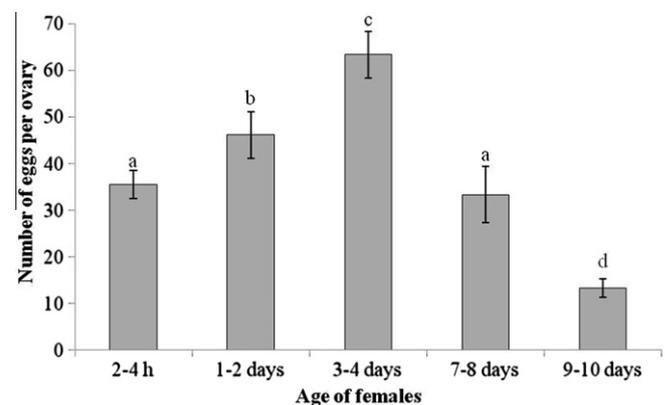
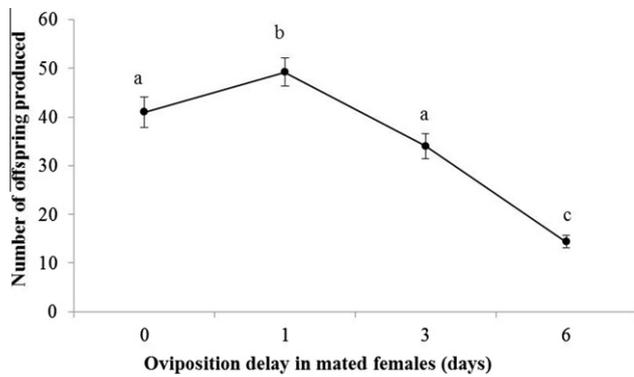


Fig. 2. Mean ( $\pm$ SE) number of mature eggs found in the ovaries of unmated naïve female *Diaeretiella rapae* of different age groups. Means with the same letter are not significantly different at  $\alpha = 0.05$  (Tukey's HSD).

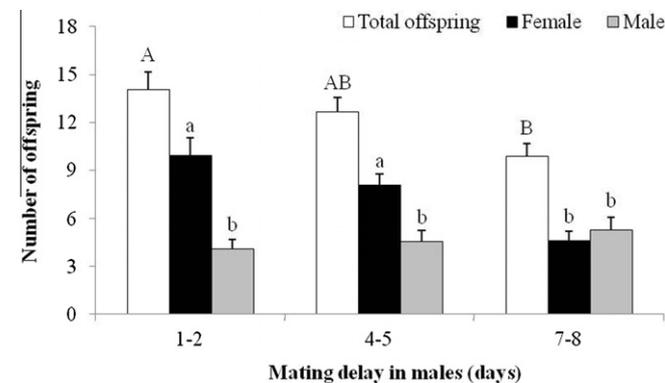


**Fig. 3.** Total number of offspring (mean  $\pm$  SE) produced by mated *Diaeretiella rapae* females which were prevented from ovipositing for different periods after their emergence. Means with the same letter are not significantly different at  $\alpha = 0.05$  (Tukey's HSD).

**Table 1**

Mean ( $\pm$ SE) number of female progeny and sex ratio of the progeny produced by mated female *Diaeretiella rapae* which were prevented from ovipositing (oviposition delay) for three different periods after their emergence. Means with the same letters within a column are not significantly different at  $\alpha = 0.05$  (Tukey's HSD).

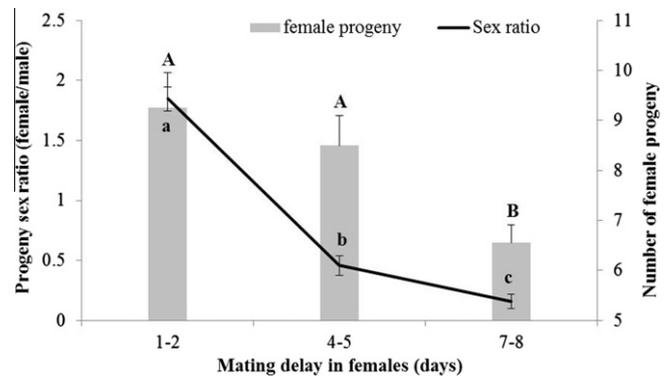
Oviposition delay (days)	Mean number of female progeny	Progeny sex ratio (female:male)
Nil	29.4 $\pm$ 2.58a	2.6 ab
1	38.7 $\pm$ 3.01 b	3.9 b
3	22.4 $\pm$ 1.69 a	2.3 a
6	7.7 $\pm$ 0.63 c	1.3 c



**Fig. 4.** Mean ( $\pm$ SE) number of male and female offspring produced by female *Diaeretiella rapae* mated with males whose mating was delayed for different periods after their emergence. Means with the same letter are not significantly different at  $\alpha = 0.05$  (Tukey's HSD). Capital letters compare the means of total offspring produced, while small letters compare the means of male and female offspring.

### 3.3. Mating delay in males and females

All females that were mated with newly emerged males produced female offspring. This confirms that male *D. rapae* are able to successfully mate and transfer viable sperm immediately upon emergence. Delay in mating did not affect the courtship capacity of males. When 7–8 day old males were paired with females, they displayed courtship immediately after pairing in a way similar to the newly emerged males, and 80% of them mated with both females. However, the duration of copulation was longer in males whose mating was delayed for 7–8 days ( $72.1 \pm 1.8$  s) compared to newly emerged males ( $58.8 \pm 1.9$  s) ( $F_{1,40} = 24.89$ ;  $P < 0.001$ ).



**Fig. 5.** Progeny sex ratio of female *Diaeretiella rapae* subjected to different periods of mating delay after their emergence. Means with the same letter are not significantly different at  $\alpha = 0.05$  (Tukey's HSD).

Mating delay adversely affected the reproductive potential of male *D. rapae*. Females mated with older males (7–8 days old) produced significantly fewer offspring than females mated with younger males ( $F_{2,31} = 4.31$ ;  $P = 0.022$ ) (Fig. 4). The mean number of female offspring produced by females was also affected by the age of the males they mated ( $F_{2,31} = 7.99$ ;  $P = 0.002$ ) (Fig. 4). However, the number of male offspring produced by females was not significantly affected by the age of their mating partner ( $F_{2,31} = 1.14$ ;  $P = 0.33$ ) (Fig. 4).

The reproductive capacity of female *D. rapae* was negatively affected when their mating was delayed. The number of offspring produced per day reduced significantly in females whose mating was delayed for a longer period (6 days) compared to when delay was short (1 day) ( $P < 0.01$ ) (Fig. 5). The sex ratio (female:male) of their offspring decreased significantly when their mating was delayed ( $F_{2,27} = 24.89$ ;  $P < 0.001$ ) (Fig. 5).

## 4. Discussion

Delay in mating and oviposition affected the reproductive fitness of *D. rapae*. The number of offspring produced by female *D. rapae* decreased when their mating was delayed. Older male *D. rapae* transferred less or lower quality sperm, which was reflected by the decrease in the resulting female offspring. Female *D. rapae* produced viable male offspring through ovipositing unfertilised eggs immediately after emergence. However, the number of offspring produced by female *D. rapae* prior to mating was less than the number of offspring produced after mating. Pre-mating oviposition can cause overproduction of males in the following generation, so the reduced oviposition rate by unmated female *D. rapae* could be a strategy to minimise the overproduction of males. Results also revealed that the number of subsequent ovipositions was also reduced when the females were deprived of hosts for a period of time, and the number of ovipositions decreased with increasing length of delay, irrespective of the mating status of the female.

Although females emerged with developed eggs, their egg load increased during their early life, suggesting that *D. rapae* is a weakly-synovigenic species (Jervis et al., 2001). The reduced oviposition and decreasing egg count in females whose oviposition was delayed suggests either deterioration or partial resorption of eggs by the females towards the end of their life. Resorption of eggs occurs in various parasitoid species, and females usually have full control over the resorption process (Guo et al., 2011; Hegazi et al., 2007; Richard and Casas, 2009). The number of eggs in the ovaries of females whose oviposition was delayed for 1 or 2 days remained unchanged, suggesting that egg resorption at a later stage of female life could be due to nutritive stress at old age (Bell

and Bohm, 1975; Rosenheim et al., 2000). Resorption of eggs reduces fecundity and is a last resort that could help a female to live longer (Jervis and Kidd, 1986). The increase in egg count early in the life of *D. rapae* females followed by later decrease, suggests that females can mature eggs but cannot produce new eggs.

Sex ratio of the progeny of mated *D. rapae* female was female-biased irrespective of the length of oviposition delay. However, the number and proportion of female progeny decreased with increasing oviposition delay. Since female *D. rapae* mate once in their life times while males mate multiple times (Kant et al., 2012d), the operational sex ratio of *D. rapae* is male-biased even when numerically more females than males are present in the population (Kant et al., 2012b). In ideal conditions (without any delay), a female will produce more female progeny in order to have only enough males to ensure that all her daughters will be mated (Ode et al., 1998). This reduces competition among her sons in finding mates, and increases the number of mates for each of her sons (Frank, 1998; Reece et al., 2004). Therefore, a reduction in the number of female offspring due to oviposition delay decreases the relative fitness of *D. rapae*. The decrease in the proportion and number of female progeny in older mothers suggests that with increasing age, female *D. rapae* may lose their capacity to fertilise their eggs, and this might be due to deterioration in the quality of sperm stored in the spermatheca of females (Reinhardt and Meister, 2000). The decrease in egg load of female *D. rapae* as they age must result in a decrease in the total number of fertilised eggs produced by those females compared to young females. This is similar to the situation in the pupal parasitoid *Nasonia vitripennis*, which produced more males as oviposition was delayed for longer (King, 1962) and the parasitoid *Microplitis rufiventris* (Hegazi et al., 2007). However, the progeny sex ratio of the egg parasitoid *Trichogramma brassicae* did not change when its oviposition was delayed for up to 25% of its life time (Fleury and Bouletreau, 1993). A short delay in oviposition (10–20% of their total life) does not affect the overall reproductive capacity of female *D. rapae*.

All females mated with newly emerged males produced female offspring, indicating that male *D. rapae* can successfully mate and transfer viable sperm immediately after emergence. Males were active during late matings and successfully mated with females despite a delay. Females mated with older males whose mating had been delayed produced fewer offspring with a lower proportion of females, suggesting that the reproductive potential of male *D. rapae* deteriorates with age. The capacity of males to transfer sperm during mating decreases with their age (Bissoondath and Wiklund, 1996), and declining numbers of female progeny indicate a decline in sperm transfer by males (Henter, 2004). Further, the number of progeny produced by females that mated with low quality males also decreased. This could be a strategy used by female *D. rapae* to produce a balanced sex ratio in progeny. Females use a similar strategy when they mate with smaller males (Kant et al., 2012d). Female age also affected the overall progeny production of females when their mating was delayed. The longer copulation duration reported from older male *D. rapae* that experienced mating delay further supports the inference of decreased efficiency of sperm transfer in older males.

Mating delay in females negatively affected their reproductive capacity. A longer delay in mating could result in oviposition of a large number of unfertilised eggs and result in the production of more males in the next generation (Hardy et al., 2007). Furthermore, the decreased proportion of female progeny produced in the mating-delay experiment could be due to deterioration of sperm quality and quantity (Damiens et al., 2003). Despite the production of a highly female-biased offspring sex ratio from post-mating oviposition, this did not compensate for the overproduction of males during pre-mating oviposition, so the overall sex ratio (female/male) remained low. We have previously shown that female

*D. rapae* can manipulate offspring sex ratio by superparasitising hosts with fertilised eggs if they encounter the same hosts during post-mating oviposition (Kant et al., 2012c).

The results of this research indicate that female *D. rapae* produce fewer offspring overall and disproportionately fewer females when oviposition or mating is delayed for a relatively long period. Decreased progeny number and decreased egg count suggest partial resorption of eggs in *D. rapae*. This partial resorption could help female *D. rapae* utilise the same resources to enhance their longevity and reutilise the nutrients for future oviposition opportunities. The decrease in the proportion of female offspring produced by mothers whose oviposition was delayed suggests that sperm stored in the spermatheca might deteriorate by the end of female's life. However, a one day delay in oviposition increased both the number of offspring and the proportion of females in *D. rapae*. Thus, in biocontrol programmes, knowing the age of the parasitoids to be released in glasshouses or in the field is important to increase their efficiency in suppressing pest population. This research suggests the use of 1–2 days old adult *D. rapae* for best results in biological control programme.

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