

# Effects of alyssum flowers on the longevity, fecundity, and sex ratio of the leafroller parasitoid *Dolichogenidea tasmanica*

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## Abstract

A laboratory experiment assessed the effect of floral food resources on the longevity, fecundity, and sex ratio of *Dolichogenidea tasmanica* (Cameron) (Hymenoptera: Braconidae), a parasitoid of leafrollers (Lepidoptera: Tortricidae). Alyssum (*Lobularia maritima* (L.), Brassicaceae) plants with flowers were compared with plants without flowers, with water available in both treatments. Adult parasitoids were provided with an excess of second-instar larval hosts, which were then reared to determine the composition of the F1 parasitoid generation. Female parasitoids with access to alyssum flowers lived, on average, seven times longer than those without flowers. Male longevity was three times greater with, than without flowers. The lifetime realised fecundity of *D. tasmanica* was also significantly increased in the presence of flowers, although this was a consequence of the increase in longevity, rather than an increase in daily fecundity. Without flowers, offspring sex ratios were strongly male biased, but when females had access to flowers an approximately equal sex ratio was produced. These results are discussed in relation to the use of flowers in agroecosystems for the conservation biological control of leafroller pests.

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**Keywords:** Alyssum; *Lobularia maritima*; Nectar; Pollen; Floral feeding; Parasitoid; *Dolichogenidea tasmanica*; Braconidae; Fecundity; Longevity; Sex ratio; Leafroller *Epiphyas postvittana*; Tortricidae; Habitat manipulation

## 1. Introduction

*Dolichogenidea tasmanica* is a solitary endoparasitoid of the larvae of leafroller moths. It originates from Australia, where its primary host is *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), but it also occurs in New Zealand where it is the most common parasitoid attacking this, and other, pest leafroller species (Charles et al., 1996; Suckling et al., 1998). Previous studies in New Zealand have investigated the possibility of enhancing the efficacy of this parasitoid by adding floral resources to apple orchards (Irvin et al., 2000) and vine-

yards (Berndt et al., 2002). These studies investigated the hypothesis that many agroecosystems lack food resources, such as nectar and pollen, required by the adult stage of many Hymenopteran parasitoids. Adding floral resources to an agroecosystem may enable certain parasitoids to increase their impact on pest populations (Gurr et al., 1998; Jervis et al., 2004; Landis et al., 2000). Without access to appropriate foods, parasitoids may suffer reduced survival, fecundity, and search efficiency (Hocking, 1967; Irvin et al., 1999; Jervis et al., 1996; Johanowicz and Mitchell, 2000; Leatemia et al., 1995; Leius, 1961; Yadav, 1985). The availability of food may also affect the offspring sex ratio of some parasitoids (Khafagi, 1998; Leatemia et al., 1995). This change in sex ratio in the presence of floral resources was observed in *D. tasmanica* in a field experiment in which flowering buckwheat (*Fagopyrum esculentum*

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Moench) was added to a vineyard system (Berndt et al., 2002). In the present study alyssum flowers (*Lobularia maritima* (L.)) are used in a laboratory experiment to further examine this effect of floral resources on the sex ratio of this species, and to investigate the effect of these resources on the longevity and fecundity of *D. tasmanica*. Alyssum was used here because it produces prolific small, white flowers with shallow corollae that are similar in size to buckwheat flowers and in their benefits to *D. tasmanica* (Irvin, 1999). In addition, the small size of alyssum plants made it possible to use live plants in laboratory cage experiments.

## 2. Materials and methods

Six replicates of each of two treatments (alyssum and control) were set up across three controlled environment rooms in a randomised block design. Alyssum treatments provided parasitoids with nectar- and pollen-producing alyssum flowers (cv. Carpet of Snow) as a food source, and control treatments had alyssum plants with the flower removed. Although flowers condition was not specifically recorded, all plants were flowering prolifically and had florets in a range of stages present throughout the experiment. Each replicate consisted of a 51 × 51 × 56 cm clear Perspex cage, with a 25 × 25 cm Terylene mesh door. Each of these cages contained one female, and two male *D. tasmanica*, leafroller larvae on artificial diet (from The Horticulture and Food Research Institute of New Zealand Ltd, Auckland, modified from Singh, 1983), water-soaked cotton wool, and an alyssum plant with or without flowers. In control treatments, flower buds were removed as they appeared on plants during the experiment. Plants in both the control and the alyssum flower treatments received the same amount of water during the experiment. Each cage was illuminated by six fluorescent tubes (three Osram L30W/77 Fluora, and three Osram L30W/11-860 Luminex Plus Daylight), which emitted daylight-equivalent spectra. Rooms were at 17 °C with a 4 °C range, and a L16:D8 photoperiod. Mean relative humidity in the rooms was 55% with a 9% range.

Parasitoids used in this experiment were laboratory-bred offspring of *D. tasmanica* reared from *E. postvittana* released and recovered at a vineyard in Canterbury, New Zealand, using methods described in Berndt et al. (2002). *Epiphyas postvittana*, from a colony maintained by The Horticulture and Food Research Institute of New Zealand Ltd, Auckland, was used as a host in the experiment and in parasitoid cultures. Parasitoid culturing was conducted under the same environmental conditions as the experiment. Parasitoids for each treatment cage were randomly selected from a collection of *D. tasmanica* of the appropriate age, with female parasitoids less than 12 h old, and males between one and two days

old. Any that appeared abnormal in their behaviour were discarded.

To increase the likelihood of mating, each female was enclosed with its assigned males in a mating cage for 24 h before being released into the larger experimental cage. These cages consisted of a cylinder of transparent plastic sheeting 15 cm high and 6.5 cm in diameter, with a fine Terylene mesh top and a Petri dish for a base. Each cage contained water-soaked cotton wool, and those in alyssum treatments also had a freshly cut alyssum flower head in a vial of water.

An excess of leafroller larvae were presented to the parasitoids in plastic rearing boxes (Clare et al., 1987) containing artificial diet. Leafrollers were reared from eggs in these boxes (approximately 200 mature eggs per box) resulting in a mean of  $156 \pm 7.3$  ( $\pm 1$  SE) larvae per box. Boxes were presented to parasitoids after 4–6 days at an average temperature of 20 °C, when the larvae were in the second instar.

Throughout the experiment, cages were checked between 08:30 and 09:30 h each day. During these checks, parasitoid deaths were recorded and female parasitoids were captured and confined in the leafroller rearing boxes inside each of the treatment cages. Parasitoids were confined in the boxes to prevent the leafroller diet drying out. Between 12:30 and 13:30 h each day, female parasitoids were released from the rearing boxes back into the main cage. After three daily four hour periods of exposure to the parasitoids, leafroller rearing boxes in the experimental cages were replaced with fresh ones. This procedure continued until the female parasitoid in each cage died. This method ensured that each female was exposed to one box of leafrollers for 4 h at a time on three consecutive days before a fresh box of leafrollers was introduced. This procedure gave female parasitoids access to approximately 156 hosts every three days. An egg load of 300 has been recorded in *D. tasmanica* with access to buckwheat flowers (Irvin, 1999), but no previous work has been done on the number of hosts this species is capable of attacking per day, so the assumption was made that the number of hosts per box was sufficient to provide an excess.

Once rearing boxes were removed from the experimental cages, they were returned to 20 °C conditions, and leafrollers were reared to either moth pupa or parasitoid cocoon. No formal observations were made of flower visiting by *D. tasmanica* in the experiment, but parasitoids were seen apparently feeding on flowers on several occasions (personal observation).

Mean parasitoid fecundity per day was calculated for each three-day period (number of parasitoid cocoons produced/number of days exposed to hosts). Sex ratio, defined as the proportion of offspring that were male, was also calculated for each three-day period separately. Data were analysed using an ANOVA model (Systat,

SPSS, 1998), with rooms treated as blocks. The model did not include a time component because no parasitoids in control cages lived past the first three-day set, so no comparison of treatments over time was possible.

### 3. Results

Alyssum flowers significantly increased the longevity of both male ( $F = 13.3$ ,  $df = 1$ ,  $P = 0.008$ ) and female ( $F = 25.3$ ,  $df = 1$ ,  $P = 0.001$ ) *D. tasmanica*. The mean longevity of female parasitoids was  $15.7 \pm 2.77$  days ( $\pm 1$  SE) with alyssum flowers, and  $2.2 \pm 0.17$  days without flowers. Male parasitoids lived for a mean of  $12.4 \pm 1.89$  days with, and  $3.6 \pm 0.53$  days without alyssum flowers. Lifetime fecundity, as estimated by the total number of offspring of each parasitoid reaching the cocoon stage, was also significantly increased by the presence of alyssum flowers ( $F = 35.8$ ,  $df = 1$ ,  $P < 0.001$ ). The mean fecundity with access to flowers was  $152.8 \pm 24.31$  cocoons, compared with a mean of  $20.2 \pm 3.89$  cocoons produced without flowers. The presence of flowers did not significantly affect the mean daily fecundity in the first three-day period ( $F = 0.2$ ,  $df = 1$ ,  $P = 0.670$ , Fig. 1), the only period for which treatments could be compared due to the early death of parasitoids in the controls. For parasitoids in the alyssum treatment, mean daily fecundity reduced over time from around 15 cocoons per day in the first three-day period, to two cocoons per day from days 25 to 27 (Fig. 1).

The offspring sex ratios of parasitoids without flowers were strongly male biased, with five of the six parasitoids producing only male offspring in the first three-day period, giving a mean sex ratio close to one (Fig. 2). Over this same period, in the presence of alyssum flowers, the sex ratio was significantly lower, at 0.6 ( $F = 9.1$ ,  $df = 1$ ,  $P = 0.017$ , Fig. 2). The offspring sex

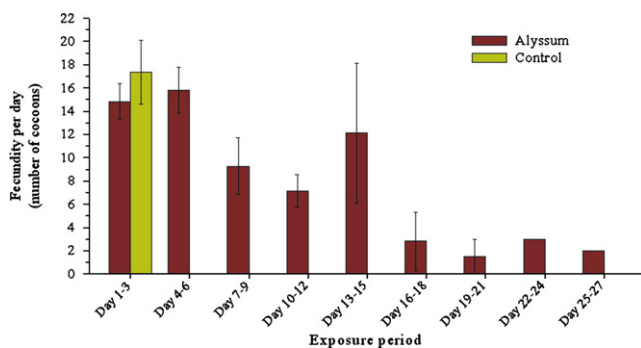


Fig. 1. Mean daily fecundity of *D. tasmanica* in alyssum and control treatments for each three-day period (for the comparison of treatments in the first period:  $P > 0.05$ ; error bars =  $\pm 1$  SE, no comparison could be made for other periods as all control parasitoids had died after three days).

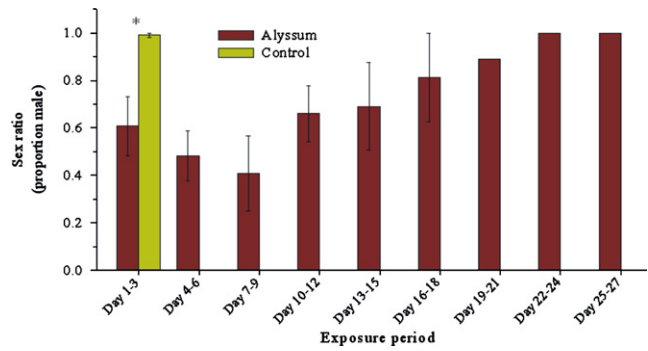


Fig. 2. Mean offspring sex ratio (proportion male) in alyssum and control treatments for each three-day period (for the comparison of treatments in the first period:  $*P < 0.05$ , error bars =  $\pm 1$  SE, no comparison could be made for other periods as all control parasitoids had died after three days).

ratio of parasitoids exposed to alyssum flowers changed over time, rising to 1 by the time the parent female reached 22 days old (eighth set, Fig. 2). The greatest proportion of females was produced between days seven and nine (Fig. 2).

### 4. Discussion

When *D. tasmanica* individuals were given only water they lived for only a few days, and had very low lifetime fecundity. With alyssum flowers as a food source, the mean female longevity was seven times greater, and the mean lifetime fecundity was eight times greater than without flowers. These results are supported by other studies which have invariably found an increase in longevity and fecundity (when it was measured) with flowers or honey as a food source, compared with water or no food (Costamagna and Landis, 2004; Gurr and Nicol, 2000; Hocking, 1967; Hodgson et al., 1993; Irvin et al., 1999; Johanowicz and Mitchell, 2000; Leatemia et al., 1995; Leius, 1961; Yadav, 1985). The mean fecundity per day in the present study did not differ between treatments for the first three-day period (Fig. 1), after which all control parasitoids had died. Therefore, the increase in lifetime fecundity with flowers was due to the positive effect of flowers on longevity (allowing parasitoids more time to attack hosts), rather than a direct increase in fecundity due to improved nutrition. This suggests that *D. tasmanica* is at least partially pro-ovigenic (Jervis et al., 2001), emerging from the cocoon with eggs already mature. A similar result was found for *Trichogramma minutum* Riley (Hymenoptera: Trichogrammatidae), in which a range of diets (including honey and water) produced a similar number of offspring in the first two days of life, yet lifetime fecundities were significantly greater with carbohydrate than with non-carbohydrate foods (Leatemia et al., 1995).

#### 4.1. Sex ratio

In this study, the sex ratio of *D. tasmanica* was very male-biased when parent female parasitoids had no access to floral resources. However, when alyssum flowers were available, the proportions of male and female offspring were closer to equal when parasitoids were young, but shifted in favour of males as they aged. An equal sex ratio is assumed to be the normal state for this parasitoid, based on that found in *D. tasmanica* reared from wild leafrollers collected in a vineyard (L.A. Berndt, unpubl.). The reduction in female production found when floral resources were unavailable in the present study supports the findings of a field experiment by Berndt et al. (2002). In that study *D. tasmanica* were reared from sentinel leafroller larvae released in vineyard plots with and without buckwheat flowers, and a significantly greater proportion of parasitoids were female in the presence of flowers than in control plots (Berndt et al., 2002). These results suggest a new mechanism by which a lack of floral resources in an agroecosystem might impact on the population dynamics, and potentially the efficiency, of a biological control agent. No research has been done to investigate the reasons behind the observed change in sex ratio, however a recent study by Costamagna and Landis (2004) found no significant effect of honey feeding on the sex ratio of *Meteorus communis* (Cresson) (Hymenoptera: Braconidae).

There are aspects of the biology of arrhenotokous parasitoids (producing females from fertilised eggs and males from unfertilised eggs, such as *D. tasmanica*) that can influence sex ratio. Whether the female is mated or not directly affects sex ratio, as virgin females produce only male offspring (Godfray, 1994). Mating success may depend on the attractiveness or mate-searching ability of the male, or the receptivity of the female, which, in turn, could be influenced by the availability of floral food. The presence of flowers could also influence mating if they are used as a site for mate location (Jervis et al., 1993). Sperm viability (Quicke, 1997), and the ability of the egg to accept sperm (King, 1962) are critical in determining the success of fertilisation, and so directly affect sex ratio. Either of these factors could potentially be affected by food availability. Sex ratio in the progeny of most Hymenoptera is under the control of the female, and may be varied to maximise her fitness (Quicke, 1997). There may be some evolutionary advantage in reducing female production when floral food is not available. There are many other factors that can influence parasitoid sex ratio, such as inbreeding, superparasitism and host size (Godfray, 1994), but these are unlikely to have been affected by the diet of adult parasitoids in this experiment. Further research is required to determine whether mating success, sperm viability or fertilisation are affected by floral feeding, and to investigate how or why this might impact on sex ratio.

#### 4.2. Implications for biological control

The presence of flowers clearly increases the longevity and fecundity of parasitoids, as shown in the present study. For *D. tasmanica* at least, increasing longevity leads directly to an increase in fecundity. Greater parasitoid fecundity has been positively associated with success in biological control of Lepidoptera (Lane et al., 1999). It therefore follows that if the presence of flowers increases *D. tasmanica* longevity in the field, a greater rate of parasitism of leafrollers should result, possibly leading to improved biological control. This remains to be demonstrated in the field, but the fact that *D. tasmanica* abundance did increase in the presence of flowers in a field experiment (Berndt et al., 2002) does support this idea. Computer modelling could be used in this situation to predict the effects of increased parasitoid fecundity on pest populations (Kean et al., 2003).

Increasing parasitoid sex ratios in favour of female offspring could lead to an increase in parasitism rate and improved biological control, as sex ratio is directly related to the intrinsic rate of increase of a parasitoid (Hall, 1993). Successful (Simmonds, 1947) and unsuccessful (Ram and Sharma, 1977) attempts have been made to select for female-biased sex ratios to create more efficient parasitoid strains for use in classical biological control. However, there are virtually no data that link altered sex ratios with improvements in biological control in the field (Hall, 1993).

### 5. Conclusion

In this study, alyssum flowers increased longevity and fecundity, and produced an apparently normal sex ratio in *D. tasmanica*, compared with no flowers. The findings regarding longevity and fecundity are consistent with other research. However, unlike some parasitoid species, the fecundity of *D. tasmanica* was reduced in the absence of food only through the reduction in longevity. The effect of food on parasitoid sex ratios has rarely been examined, although the results of a field experiment by Berndt et al. (2002) support the present findings. Without further research, no conclusions can be drawn regarding the mechanisms by which sex ratio manipulation is affected by floral food in *D. tasmanica*. The results of this experiment show that the availability of food for adult parasitoids is critical for their survival, and therefore plays an important role in the effectiveness of a parasitoid as a biological control agent.

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