

Flower color affects tri-trophic-level biocontrol interactions

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Abstract

The adults of many parasitoid species require nectar for optimal fitness, but very little is known of flower recognition. Flight cage experiments showed that the adults of an egg parasitoid (*Trichogramma carverae* Oatman and Pinto) benefited from alyssum (*Lobularia maritima* L.) bearing white flowers to a greater extent than was the case for light pink, dark pink or purple flowered cultivars, despite all cultivars producing nectar. Survival and realised parasitism on all non-white flowers were no greater than when the parasitoids were caged on alyssum shoots from which flowers had been removed. The possibility that differences between alyssum cultivars were due to factors other than flower color, such as nectar quality, was excluded by dying white alyssum flowers by placing the roots of the plants in 5% food dye (blue or pink) solution. Survival of *T. carverae* was lower on dyed alyssum flowers than on undyed white flowers. Mixing the same dyes with honey in a third experiment conducted in the dark showed that the low level of feeding on dyed flowers was unlikely to be the result of olfactory or gustatory cues. Flower color appears, therefore, to be a critical factor in the choice of plants used to enhance biocontrol, and is likely also to be a factor in the role parasitoids play in structuring invertebrate communities.

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1. Introduction

Color is one of the most important cues for insect recognition of flowers (Chittka and Menzel, 1992; Kevan et al., 1996; Menzel and Backhaus, 1991) and is well studied in relation to pollination biology (Heiling et al., 2003; Menzel and Shmida, 1993). It is well documented that hymenopterans are important insect pollinators (Brown et al., 1998) and they discriminate between flowers by using signals such as color, size, shape, patterns, odor, and other characteristics (Gumbert, 2000). In addition, pollinators have demonstrated a capacity for associative learning in relation to specific colors and rewards (Brown et al., 1998; Chittka and Menzel, 1992; Oliai and King, 2000) and this ability allows them to identify and exploit profitable food sources (Chittka and Menzel, 1992).

Flowers are also important to non-pollinating insects such as many biological control agents. Parasitoids visit flowers for food and there is increasing evidence that many insect predators and parasitoids require access to nectar and/or pollen (Jervis et al., 1993; Wäckers, 1994). Habitat manipulation approaches such as strips of flowers are sometimes used to maximise their biocontrol potential (Landis et al., 2000). Adult parasitoids require food as an energy source for flight (Elton, 1966) or for egg production in synovigenic species (Jervis et al., 1996). The ability of parasitoids to locate nectar sources is important in biological control agents, but despite this relatively little research has been done on the importance of visual cues in the food/host location processes of parasitoids compared with the role of chemical stimuli (Takasu and Lewis, 1996; Weseloh, 1981). Some parasitoids have been shown to respond to color and other visual cues (Vinson, 1976; Wäckers and Lewis, 1994).

It is well recognised in tri-trophic systems, that the first trophic level (crop) plays a significant role in

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mediating ecological interactions between hosts and parasitoids (Takabayashi et al., 1998; Verkerk et al., 1998). Plant attributes such as provision of nectar and pollen can affect abundance, survival, fecundity, and development of natural enemies (Cortesero et al., 2000). If, therefore, flower color is important for the use of floral resources by parasitoids, such effects need to be better understood for optimising habitat manipulation approaches in conservation biological control.

Trichogramma carverae Oatman and Pinto (Hymenoptera: Trichogrammatidae) is one of the most important natural enemies of the light brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae), a serious insect pest of Australian grapevines (Glenn and Hoffmann, 1997). Crop loss can amount to \$2000/ha in a season, especially in the cooler grape growing areas (Buchanan, 1977). In Australian vineyards, *T. carverae* is released to control *E. postvittana* (Glenn and Hoffmann, 1997), but at a cost of Aus\$ 45/ha for each of the two to three releases required per season (Gurr et al., 1998). The longevity of *Trichogramma* spp. is very short when no sugar source is available (Newton and Odendael, 1990) and fewer hosts are parasitised by unfed females (Ashley and Gonzalaz, 1974). Gurr and Nicol (2000) demonstrated a dramatic reduction in survival of *T. carverae* when deprived of carbohydrate. It is important, therefore, that factors affecting the availability of nectar for *T. carverae* be studied.

As an endemic Australian egg parasitoid *T. carverae* is a particularly important target for enhancement by conservation biological control because inundative releases are already being used to augment natural populations in vineyards. These mass releases are, however, expensive and provision of appropriate adult food offers scope to increase the impact of a given release on pest densities though maximising fecundity, longevity, and other aspects of parasitoid fitness. The selection of flower species is important to the success of the provision of nectar resources in habitat manipulation (Berndt, 2002; Gurr et al., 1998). Factors considered important in floral attraction of insect natural enemies include nectar availability (Idris and Grafius, 1995) and accessibility (Wäckers et al., 1996) and the duration of flowering (Lövei et al., 1993), but very little attention has been given to flower color.

The present study investigated the effect of flower color as a factor in the biological control efficacy of *T. carverae*. We measured survival of and parasitism achieved by this trichogrammatid parasitoid when it had access to different colored alyssum flowers and a control treatment (shoots of white flowering alyssum from which flowers were removed) under no-choice conditions. We investigated whether cultivar effects may have been associated with nectar quantity by determining the numbers of flowers without obvious nectar. To investi-

gate whether flower color was responsible for the differences observed in insect performance, we conducted an experiment involving dying plants of the white flowering cultivar of alyssum. Finally, we tested whether the non-preference for dyed alyssum flowers was the result of negative olfactory or gustatory stimuli from the dyes.

2. Materials and methods

2.1. *Alyssum* flower color experiment

Capsules containing paper substrates bearing *Sitotroga cerealella* Oliver eggs parasitised by *T. carverae* used in this experiment were purchased from Bugs for Bugs, BioResources Pty, Mundubbera, Queensland, Australia. Capsules were incubated at 28 °C. After *T. carverae* started to emerge in an “indicator vial,” all of the capsules for this experiment were taken out of the incubator and kept at room temperature to await adult eclosion approximately 24 h later.

Alyssum, *Lobularia maritima* L. (Cruciferae) plants used in these studies were purchased from a nursery (Oasis Horticulture Pty, Wimalee, Australia). The experimental design was a randomised block with four replicates and five treatments. In this experiment, plastic vials (5.5 × 4.5 cm) were used as flight cages and each held three cut alyssum shoots bearing either white, light pink, dark pink or purple flowers (cultivars: Small Flower White, Small Flower Pink, Plum Crazy, and Small Flower Purple, respectively). In all flowering treatments, each shoot had sufficient buds to ensure continuous flowering throughout the experimental period. A control treatment used shoots from white-flowered alyssum from which flowers and unopened flower buds were removed. This treatment was used to control for the effect of plants on the microclimate within cages. The cut ends of shoots were placed immediately in tap water and the experiment began within 5 h of shoot collection. The cut end of each shoot was passed through a small circular hole (1 cm diameter) in the bottom of each plastic vial into water contained in a second vial (11 × 2.5 cm) beneath the first. Shoots were sealed into the holes with non-setting adhesive (Blue-Tack) to prevent insect escape. The top of the upper vial was then sealed with a sheet of tissue paper held in place with a rubber band. The units were supported in laboratory racks. Each capsule (bearing *S. cerealella* eggs parasitised by *T. carverae*) was cut into eight segments, bearing approximately 125 eggs. One of these segments was placed into each flight cage via a hole (2 × 1 cm) in its wall, which was then sealed with same adhesive. The experiment was laid out on a laboratory bench top. The numbers of live wasps in each flight cage was recorded every 24 h until no more live *T. carverae* were recorded.

To measure parasitism rate, *E. postvittana* eggs were obtained from the Department of Natural Resources and Environment, Victoria, Australia. Sentinel cards were prepared by cutting the plastic oviposition substrate into sections, each bearing one intact egg mass, and stapling each section to a yellow paper sheet (5×1 cm). Because acceptance of *E. postvittana* eggs by *T. carverae* is affected by age of host (Glenn and Hoffmann, 1997), we used only green (younger) eggs. Microscopic examination ($10\times$) was used to count the number of eggs in each intact mass and this was recorded on each paper sheet. Each card had a mean of 20.96 eggs (range 5–57; half bearing 13–27 eggs). On every 3rd day after *T. carverae* emergence, one sentinel egg card was placed in each flight cage (except cages where no live adults were present) to allow *T. carverae* oviposition and was recovered after 24 h. Egg masses were subsequently incubated at 23°C until parasitized eggs became black and could be counted. Daily maximum and minimum temperatures were recorded and temperature ranged from 20.1 to 23.4°C with a relative humidity of 56% (measured by wet and dry bulb thermometer readings).

A square root transformation, $\sqrt{(x + 0.5)}$, was used for insect survival data and the effect of flower color treatments tested by a repeated measures approach, multivariate analysis of variance (MANOVA). Because it was not possible to include days when all replicates of one treatment were zero in the MANOVA, only the first 8 days after the peak in insect counts were analysed, and not the following 6 days when no *T. carverae* were living in one or more treatments. The significance of differences between treatments and days were determined using *F* tests, although an *F* test in MANOVA is only an approximation to the *F*-distribution. Exponential curves of the form $y = A + BR^x$ (where x = number of days, y = number of live insects, A , B = linear parameters, R = survival rate) were also fitted to the data (omitting dates before the date with maximum wasp numbers) to compare differences in position (A), slope (B), and curvature (R) for each treatment. First, an overall curve was fitted, then a set of curves with a different position (A) for each treatment, after that a set of curves with different position and slope (A and B) for each treatment and finally a set of curves with all (A , B , and R) parameters separate. The steps defined above were accomplished automatically using the standard module for comparing non-linear regression in GenStat release 6.1. However, where curvature, representing the key biological parameter of insect survival, differed between treatments, comparison of the linear parameters becomes irrelevant. Percent variance accounted for the final model is shown in the graph as adjusted R^2 .

The number of eggs parasitized was calculated per cage and then analysed using MANOVA to test for flower color treatment effects. The *L. maritima* without-

flower treatment was not included because no parasitism was recorded on any date. Data from day 12 of the experiment were not included in the analysis because parasitism was recorded only in the white-flower treatment from that date. For all of the above analyses, GenStat Sixth Edition (GenStat Committee, 2002) was used.

2.2. Nectar availability test

Flowers of each cultivar were examined with a microscope at $20\times$ magnification and nectar was recorded as present or absent. A total of 23 white, 8 light pink, 14 deep pink, and 11 purple flowers were examined. The flowers used came from the same plants from which shoots were taken for other experiments. Presence/absence data were analysed with a χ^2 test using GenStat Sixth Edition (GenStat Committee, 2002) to test for differences between cultivars.

2.3. Dyed alyssum flower experiment

This experiment sought to determine whether flower color is responsible for the differential effects on *T. carverae*. Plant and insect material was sourced as described above. Three treatments replicated four times were employed in a randomised block design. White-flowered alyssum plants were removed from their pots and soil washed from their roots before being placed into water only or water with 5% food dye (pink or blue food coloring; Queen Fine Foods Pty, Queensland, Australia). After 24 h, white flowers had assumed colors that to the human eye were similar to those of the naturally colored flowers. Three flower-bearing shoots were cut from plants of each treatment (i.e., dyed pink, dyed blue or undyed) and placed in flight cages (vials) as previously described. A segment of capsule bearing eggs parasitised by *T. carverae* was also added and each vial sealed. In this experiment, the undyed white flowering treatment served as a comparison treatment. The experiment was laid out on a laboratory bench top. The number of live *T. carverae* present in each cage was recorded every 24 h until all insects had died. Daily maximum and minimum temperatures were recorded and temperature ranged from 19.0 to 22.3°C with relative humidity of 52% (measured by wet and dry bulb thermometer readings).

Insect survival data were square root transformed $\sqrt{(x + 0.5)}$ before carrying out MANOVA for the first five dates when there were live *T. carverae* in each treatment. The significance of differences between treatments and days were determined using *F* tests. Exponential curves were fitted to the data, omitting the first date (when wasps were still eclosing) as day 2 had maximum wasp numbers. Exponential survivorship curves were fitted to each treatment as in experiment 2.1.

GenStat Sixth Edition (GenStat Committee, 2002) was used for all analyses.

2.4. Dyed honey experiment

Insect material and food dye was sourced and purchased as described above. A randomised block design with five replicates and four treatments was housed in a sealed plastic box (38 × 25 × 14 cm) in which water maintained the relative humidity above 90% (measured by wet and dry bulb thermometer readings). The box was held at 28 ± 1 °C in an unlit incubator. Honey solution (10%) was dyed with the same dyes as above (dye concentration 5%) and treatments were 10% honey, 10% honey + 5% blue dye, 10% honey + 5% pink dye, and water. The water control and undyed honey solution served as reference treatments against which the dyed treatments were compared. Ten adult *T. carverae* (<24 h after eclosion) were released in each vial (5.5 × 4.5 cm). *T. carverae* adults were transferred to the flight cages (vials) using gelatine capsules (size 00) (Tyco Healthcare Pty, Sydney, NSW, Australia) as described below to avoid the need for the use of anaesthesia allaying possible deleterious effects on behaviour or longevity. Within 24 h of emergence, *T. carverae* do not fly (personal observation). Young adults were put on a white paper sheet (for ease of visibility) and each adult covered with half of a gelatine capsule. Adults crawled upwards inside the capsule, which was then lifted up and sealed with the other half of the capsule. Adults were introduced into flight cages by separating the capsule halves and tapping the half containing the insect against a hole (2 × 1 cm) in the vial's wall. After adding 10 adults, the hole was sealed with same adhesive as above and examined under a microscope (10×) to confirm that 10 adults were present. Through this hole the diet, on soaked cotton wool, was inserted every 2nd day. The tops of the vials were sealed as above. Each replicate was inspected every 24 h until no live *T. carverae* were recorded. Inspections took place under red light to avoid the insects receiving any visual cues from the diet.

Count data were square root transformed $\sqrt{(x + 0.5)}$ and a MANOVA was conducted using the first six dates. Differences between treatments and times were tested using *F* tests. Exponential survivorship curves were fitted to the data for each treatment as in experiment 2.1. GenStat Sixth Edition (GenStat Committee, 2002) was used for these analyses.

3. Results

3.1. Alyssum flower color experiment

The MANOVA analysis of *T. carverae* survival showed significant interaction of treatment and time

(days) ($F = 3.61$; $df = 20, 32$; $P = 0.002$) (Fig. 1). With access to white flowers, adults were evident for 13 days; on light pink, adults were evident for 10 days; and in other treatments, no adults were evident after day 8. Fitted exponential curves for treatments differed significantly in curvature ($F = 19.20$; $df = 4, 234$; $P < 0.001$). The daily survival rate (survival rate ± SE) of *T. carverae* in the white alyssum (0.913 ± 0.024) was significantly higher than the other treatments (light pink, dark pink, purple, and stem from which white flower were removed), 0.689 ± 0.035; 0.704 ± 0.030; 0.640 ± 0.033; and 0.672 ± 0.030, respectively.

Parasitism rates were significantly higher in the white-flower treatment than in other treatments on days 3 and 6 ($F = 14.37$; $df = 4, 12$; $P < 0.001$ and $F = 6.73$; $df = 4, 12$; $P = 0.004$, respectively) (Fig. 2). The MANOVA results showed significant ($F = 3.66$; $df = 9, 17$; $P = 0.010$) interaction between treatment and time (days). Parasitism had declined markedly in the white-flower treatment by the time of the 9th and 12th days, but no parasitism was recorded in other treatments at this time.

3.2. Nectar availability test

The proportions of flowers without nectar (2/23, 1/8, 1/14, and 1/11 for the white, light pink, dark pink, and purple, respectively) did not differ significantly ($\chi^2 = 0.15$; $df = 3$; $P = 0.985$).

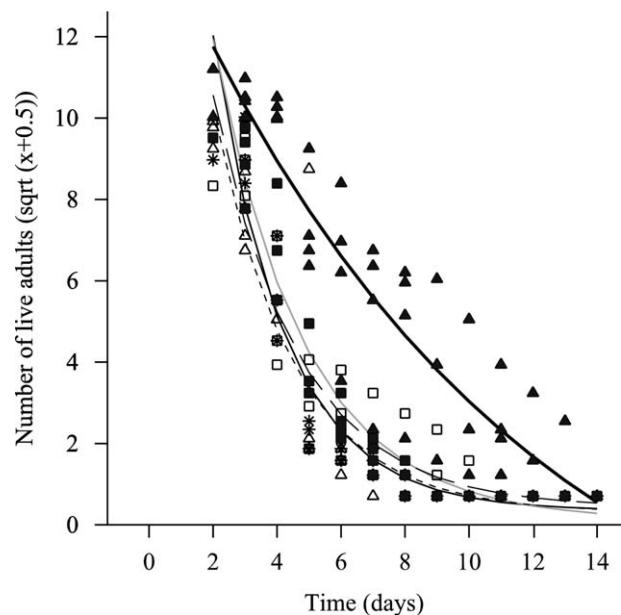


Fig. 1. *T. carverae* adult emergence and subsequent survival when confined with different colored alyssum flowers or with shoots of the white-flowered cultivar with flowers removed: —▲—, white, flowers present; - - -△- - -, white, flowers removed; - -□- - -, light pink, flowers present; —■—, dark pink, flowers present; and —*—, purple, flowers present. Adjusted $R^2 = 90.2\%$. Points denote treatment means and lines denote fitted relationships.

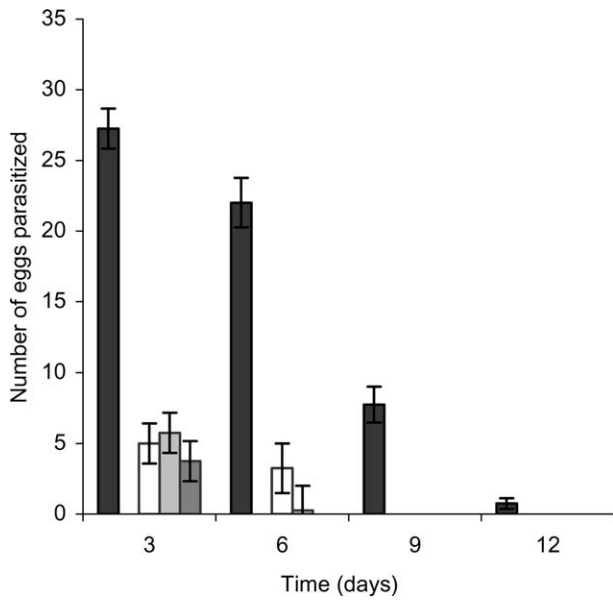


Fig. 2. Parasitism rate of *E. postvittana* eggs by *T. carverae* for each egg release date when provided with different colored alyssum flowers: ■, white, flowers removed (zero for all dates); □, light pink, flowers present; ▒, dark pink, flowers present; and ■, purple, flowers present. Bars show the standard errors.

3.3. Dyed alyssum flower experiment

The survival of *T. carverae* showed a significant interaction between treatment and time (days) ($F = 9.86$; $df = 4, 10$; $P = 0.001$) (Fig. 3). When caged on non-dyed

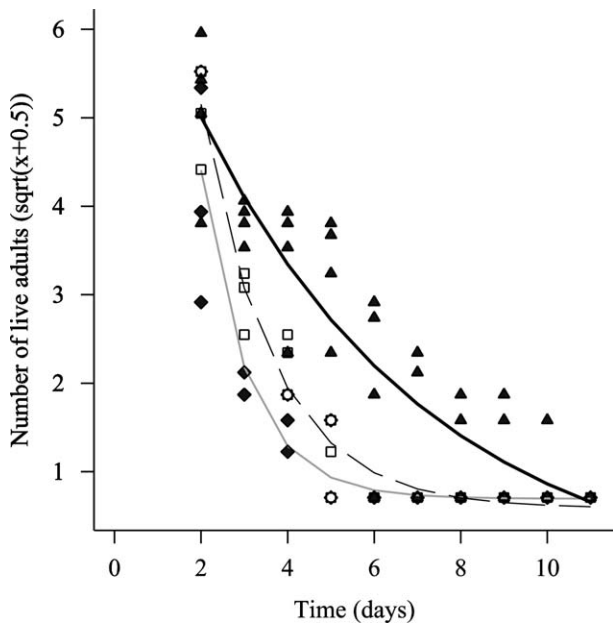


Fig. 3. *T. carverae* adult emergence and subsequent survival when confined with dyed and undyed white alyssum flowers: —▲—, undyed white alyssum flowers; -□-, dyed pink alyssum flowers; and —◆—, dyed blue alyssum flowers. Adjusted $R^2 = 89.6\%$. Points denote treatment means and lines denote fitted relationships.

white alyssum flowers, adults were evident for 10 days, but in treatments in which white flowers were dyed either pink or blue, no adults were evident after day 5. Fitted exponential curves for treatments differed significantly in curvature ($F = 24.50$; $df = 2, 111$; $P < 0.001$). *T. carverae* caged with non-dyed white alyssum had a significantly higher survival rate (0.830 ± 0.038) than in the dyed pink (0.545 ± 0.042) and dyed blue (0.400 ± 0.058) treatments.

3.4. Dyed honey experiment

Using MANOVA for the first six dates did not show significant ($F = 0.83$; $df = 18, 20$; $P = 0.65$) interactions between treatments and time. The survival of *T. carverae* did not differ significantly between treatments (Fig. 4).

Fitted exponential curves for treatments differed significantly in curvature ($F = 8.24$; $df = 3, 168$; $P < 0.001$). The survival rate of *T. carverae* in the water treatment (0.302 ± 0.097) was significantly lower than the other three treatments (10% honey, 10% honey + 5% blue, and 10% honey + 5% pink), 0.893 ± 0.070 ; 0.766 ± 0.068 ; 0.695 ± 0.070 ; and 0.302 ± 0.097 , respectively.

4. Discussion

The present study is the first to show an effect of flower color on a trichogrammatid and is likely to have

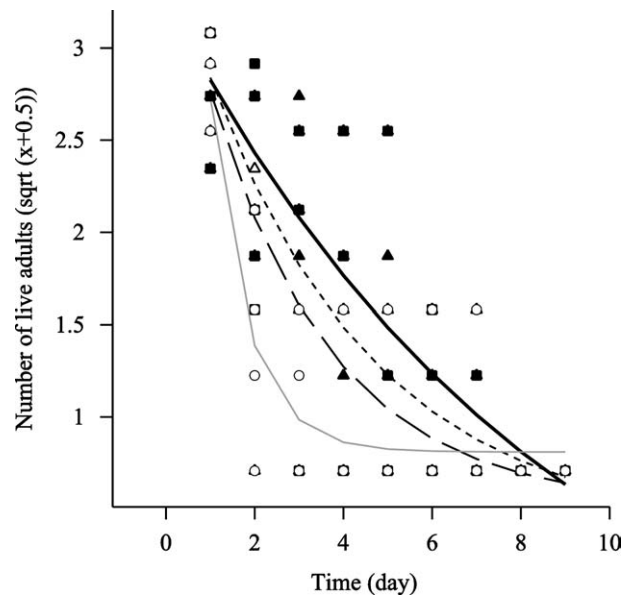


Fig. 4. *T. carverae* adult survival with dyed honey, undyed honey and water as food sources: —▲—, undyed 10% honey; -△-, 10% honey + 5% pink; - - - ■ - - - -, 10% honey + 5% blue; and —○—, water. Adjusted $R^2 = 73.6\%$. Points denote treatment means and lines denote fitted relationships.

implications for the biological control efficacy of *T. carverae*. The survival and realised parasitism of *T. carverae* were significantly greater with access to white flowers than with alyssum cultivars with flowers of other colors and a control treatment (shoots of white flowering alyssum from which flowers and flowering buds were removed). The presence of white flowers is obviously important for *T. carverae*. Kevan (1973) reported Ichneumonidae visited white flowers though other researchers (Idris and Grafius, 1997; Oliai and King, 2000; Wardle, 1990) have reported that during flower selections, parasitoid were not guided by flower color. Lukianchuk and Smith (1997) examined the foraging behavior of *Trichogramma minutum* while on artificial and natural surfaces and concluded that foliage color did not influence female *T. minutum*. Similarly, Keller (1985) demonstrated that it is unlikely that female *Trichogramma* spp. were influenced by visual characteristics because they are polyphagous and host plant visual characteristics varied greatly.

Parasitic Hymenoptera may use color contrast cues. Wäckers (1994) showed that food-deprived *Microplitis croceipes* parasitoids preferred yellow targets when foraging, while sugar-fed individuals preferred green leaves. In the current experiment, performance of *T. carverae* was greatest in the presence of white flowers. One possible reason for this effect is that white colored flowers may have given the greatest contrast against green foliage. The reflectance peak of most green leaves is generally lower than that of white flowers (Kevan et al., 1996).

Results demonstrate that choice of cultivar (within a plant species) is potentially important, leading to outcomes that range from a marked benefit to parasitoid fitness to no benefit. The cultivar effects observed could result if the nectar quantity of the white flowering cultivar is superior to that of other cultivars, and not directly related to flower color. To investigate this, the number of flowers without obvious nectar was determined for each cultivar, but the proportions did not differ significantly. Further studies involved dying plants of the white flowering cultivar of alyssum. The survival of *T. carverae* was greater on non-dyed white alyssum than dyed flowers of white alyssum. This result shows that factors such as the nectar quality were not at play and suggests that *T. carverae* uses flower color as an important visual cue. Beach et al. (2003) demonstrated that nectar use may be influenced by gustatory responses and suggested that some food sources act as mild feeding deterrents. Similarly, Wäckers (1994) found that parasitic Hymenoptera showed innate responses to food odor. It is therefore possible that the dyes used to manipulate flower colors in the present study were responsible for impaired *T. carverae* survival in blue- and pink-dyed treatments. In the follow-up experiment, however, in which honey solution was dyed, survival of

T. carverae did not differ when they fed blue- or pink-dyed honey solution and non-dyed honey solution. Survival was significantly lower in the water control treatment. Collectively, these results suggest that *T. carverae* performance on dyed alyssum flowers was the result of visual rather than olfactory or gustatory cues.

Accordingly, cultivar choice influences profoundly the use of ‘floral subsidies’ (a type of food resource subsidy) (Polis and Strong, 1996) by *T. carverae*. Resource subsidies can enhance natural enemy performance in biological control (Kean et al., 2003) via effects on longevity (Heimpel et al., 1997; Johanowicz and Mitchell, 2000), fecundity (Yu et al., 1984), female-based sex ratio of parasitoid offspring (Berndt et al., 2002), and spatial distribution (Thomas et al., 1992). Knowledge of color discrimination in *T. carverae*, as well as other natural enemies, is critical for the development of optimal habitat manipulation strategies. Overall, our results indicate that flower color is important for *T. carverae* and, because of the observed effect on survival and parasitism, that this may affect biological control efficacy. Such effects are unlikely to be confined only to this trichogrammatid species or this family and further work with Hymenoptera and other flower-feeding biological control agents is warranted. Providing resource subsidies (Polis and Strong, 1996) to parasitoids and predators is an effective and fast-expanding component of conservation biocontrol (Landis et al., 2000). Success of ‘classical’ biological control has been only 10% from the 1880s to the close of the 20th century (Gurr et al., 2000). Identifying and addressing constraints on biological control agent performance offers scope for increasing the success rate. The ecological aspects of biological control need to be better understood, and the role of flower color in tri-trophic-level interactions is clearly important and merits further research.

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