Potential for Sugar Sprays and Flowering Plants to Increase Parasitism of White Grubs (Coleoptera: Scarabaeidae) by Tiphiid Wasps (Hymenoptera: Tiphiidae)

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ABSTRACT We examined the effects of supplemental food sources on parasitism of turf-infesting white grubs (Coleoptera: Scarabaeidae) by tiphiid wasps (Hymenoptera: Tiphiidae). Survival of spring active *Tiphia vernalis* Rohwer and late summer active *Tiphia pygidialis* Allen, parasitoids of Japanese beetle, *Popillia japonica* Newman, and masked chafer, *Cyclocephala* spp., grubs, respectively, was significantly increased when wasps were provided with 10% sugar water in the laboratory. Presence of a grub for host feeding did not affect wasp longevity. Sugar sprays applied directly to turf were examined as a method for increasing grub parasitism rates. Large numbers of *T. pygidialis* visited turf sprayed with sugar water to feed. Parasitism of *Cyclocephala* spp. grubs by *T. pygidialis* was reduced in sugar-sprayed turf, but higher in turf plots located near sugar-sprayed turf. *T. vernalis*, which feeds on homopteran honeydew secretions, was never observed feeding on sugar-sprayed turf, nor did such treatments affect its parasitism of *P. japonica* in or near sugar-sprayed turf. Gardens of spring- or fall-blooming flowering plants were established and monitored to determine whether particular species might attract *Tiphia* spp. No *T. pygidialis* were observed feeding on flowers in fall-blooming gardens. Large numbers of *T. vernalis* were observed feeding on nectar from peony, *Peonia lactiflora* Pallas, in the spring-blooming garden. When replicated plantings of *P. lactiflora* were established in a stand of turf, parasitism of *P. japonica* was significantly higher near the peonies. Incorporating such nectar-producing flowers into a landscape may increase parasitism of *P. japonica* by *T. vernalis*.

KEY WORDS *Tiphia vernalis*, *Tiphia pygidialis*, white grubs, supplemental food sources, conservation biological control

AVAILABILITY OF FOOD FOR PARASITOIDS is important for successful biological control (Beirne 1962, Leius 1967, van Lenteren et al. 1987) because food can attract and retain natural enemies in an area (Evans and Swallow 1993, Jacob and Evans 1998) and increase their longevity and fecundity (Baggen and Gurr 1998, Jacob and Evans 2000, Foster and Ruesink 1984, Idris and Grafius 1995). Once fed, parasitoids may spend more time searching for hosts near the food source (Hagen 1986, Lewis et al. 1998).

As interest in biological control has increased, the potential benefits of providing supplemental food sources for parasitoids have received much attention. Flower feeding, which is common among the parasitic Hymenoptera (Jervis et al. 1993), can increase the longevity and fecundity of adult parasitoids, potentially leading to enhanced parasitism of pest insects near floral plantings (Leius 1967, Baggen and Gurr 1998). Parasitoids also may feed on honeydew produced by aphids and scale insects, which can increase parasitoid longevity (Clausen et al. 1933, Hagen 1986, England and Evans 1997). Artificial honeydews, in the form of sugar sprays, have been used to enhance the effectiveness of predaceous insects in the field (Hagen 1986). However, only a few studies (e.g., Jacob and Evans 1998) have demonstrated an increase in the field performance of a parasitoid after application of food sprays (Thompson and Hagen 1999).

Two univoltine species of *Tiphia* are abundant on golf courses and other managed turf sites throughout Central Kentucky (Rogers and Potter 2002a,b, 2003). Adults of *Tiphia vernalis* Rohwer are active in Kentucky from mid-April through early June, parasitizing overwintered third instars of the Japanese beetle, *Popillia japonica* Newman. *T. vernalis* was released in the United States during the 1920s in attempts to control the spread of Japanese beetles, which had been accidentally introduced a few years earlier (Gardner and Parker 1940). *Tiphia pygidialis* Allen is a native species that parasitizes third instars of masked chafers, *Cyclocephala lurida* Bland and *Cyclocephala borealis* Arrow, from mid-August through early October in Kentucky.

The current study examined whether providing supplemental foods (i.e., flowering plants or sugar sprays) to a landscape would enhance parasitism of *P. japonica* and *Cyclocephala* spp. grubs by *T. vernalis* and *T. pygidialis*, respectively. This premise was based on early work with exotic species of *Tiphia* that anecdotally described them as primarily blossom and honeydew feeders (Clausen et al. 1927, King and Holloway 1930, Gardner and Parker 1940). Gardens of spring- and fall-blooming flowers were established and monitored for visiting *T. vernalis* and *T. pygidialis* to determine which species of flowers are frequented by the wasps in Kentucky. Flowers found to be attractive to tiphiids in our study might then be incorporated into landscapes as part of a sustainable strategy for white grub control. In related work (Rogers and Potter 2002a,b, 2003), we have collected large numbers of *T. vernalis* and *T. pygidialis* feeding on sugar water sprays applied to the foliage of trees, low-growing shrubs, or turf. Based on these observations, we also investigated whether such supplemental food sprays applied to turf could be used to increase grub parasitism rates in a localized area.

Materials and Methods

Collection and Handling of Parasitoids and Grubs. Female *T. pygidialis* and *T. vernalis* were collected from golf courses in central Kentucky. *T. pygidialis* were collected during late August 2000 by spraying 1-m^2 plots of turfgrass with a 10% sugar water solution to thoroughly wet the grass blades. A hand-held vacuum (BioQuip, Rancho Dominguez, CA) was used to collect wasps found feeding on the sugar-sprayed grass. *T. vernalis* were collected during May 2001 in a similar manner except that a 10% sugar water solution was sprayed on the foliage of trees bordering areas of turf.

Host grubs were collected from beneath turf at local golf courses and sod farms. For tests with *T. pygidialis*, third instars of *Cyclocephala* spp. were collected in late August and September 2000. For experiments with *T. vernalis*, overwintered third instars of *P. japonica* were collected in early May 2001. Grubs were held in plastic containers (26.5 by 19.5 by 10 cm) containing a 1:1 mixture of autoclaved soil and peat moss at room temperature (22–24°C) until used in experiments.

Effects of Sugar Water and Host Feeding on Wasp Longevity. The effects of sugar water on longevity of field-collected *T. vernalis* and *T. pygidialis* were examined during the spring and fall, respectively. Twenty female wasps were confined individually in 118-ml plastic cups (Solo, Highland Park, IL) half-filled with moist autoclaved soil and provided with a piece of dental wick soaked in a 10% sugar water solution. A second group of 20 wasps was confined in individual cups of similar soil and provided with a dental wick soaked in distilled water. A lid was placed on each container and new dental wicks were provided each day.

During the oviposition process, some *Tiphia* species host feed by biting off one leg from the temporarily paralyzed grub and imbibing hemolymph produced from the wound (Clausen et al. 1932). Both *T. vernalis* and *T. pygidialis* host feed in this manner (M.E.R., unpublished data). Host feeding by parasitoids is usually done to produce more eggs but may also increase adult longevity (Quicke 1997). To account for any effects host feeding may have on longevity of *T. pygidialis and T. vernalis,* two additional treatments were included in which all wasps received a host grub, with one group also receiving a piece of dental wick soaked in sugar water, whereas the other received a dental wick soaked in distilled water. Each day both the dental wicks and the grubs were replaced. Containers with wasps were held at room temperature and a photoperiod of 14:10 (L:D) h. Effects of sugar water, presence or absence of a grub for host feeding, and their interaction on longevity of wasps were compared using factorial analysis of variance (ANOVA) (Analytical Software 2000).

Effects of Sugar Sprays on Grub Parasitism. Field experiments were conducted over a period of three field seasons (2000–2002) to determine whether supplemental food sprays can enhance grub parasitism rates by increasing local *Tiphia* abundance. In the first year, an experiment was designed to determine whether parasitism of *Cyclocephala* spp. grubs by *T. pygidialis* can be increased by application of sugar water sprays directly to grub-infested turf. On 15 August 2000, 12 pairs of turf plots were established in a stand of Kentucky bluegrass, *Poa pratensis* L., at the University of Kentucky Spindletop Research Farm and on a central Kentucky golf course. The turf stand at both study sites was mowed weekly at 5-cm height and irrigated as necessary to maintain vigor. Each plot consisted of a polyvinyl chloride (PVC) ring (39.0 cm in diameter by 10.2 cm in height) driven into the turf enclosing an area of 0.12 m^2. There was 1-m distance between the plots in each pairing and a minimum of 30 m between pairs of plots. Twenty third instar of *Cyclocephala* spp. were placed onto the surface of the turf within each plot and allowed to burrow into the turf. One plot in each pair was then sprayed with 150 ml of a 10% sugar water solution, whereas the other was left untreated. Every 2 d, the sugar-sprayed turf was retreated. To confirm that wasps were visiting the treated plots to feed, visual counts of the number of *T. pygidialis* landing and feeding on the turf sprayed with sugar water versus the untreated turf were made on five dates. After 14 d, the turf within each plot was excavated to a depth of 20 cm and all parasitized- and nonparasitized grubs and *Tiphia* cocoons were recovered to determine rate of grub parasitism. Paired *t*-tests were used to compare parasitism rates in each treatment (Analytical Software 2000).

In the second and third years, we tested the hypothesis that proximity between a food source and host larvae enhances parasitism rate by testing whether grub parasitism rates decline as distance from sugar-sprayed turf increases. Two experiments, conducted in spring 2001 and 2002, tested parasitism of *P. japonica* by *T. vernalis.* On 10 May 2001, six blocks of 13 plots were established by implanting 78 PVC rings (39.0 cm in diameter by 10.2 cm in height) into a stand of Kentucky bluegrass at the University of Kentucky Spindletop Research Farm. Mowing and irrigation were as described above. In each block,

Table 1. Plant species established in the spring garden and monitored for visits by spring active *Tiphia* spp.

Plant species	Common name	Family
Astilbe x arendsii	Bridal veil	Saxifragaceae
Campanula persicifolia L.	Peach-leaved bellflower	Campanulaceae
Centaurea montana L.	Mountain bluet	Asteraceae
Convallaria majalis L.	Lily of the valley	Liliaceae
Geranium endressii Gay	Cranesbill, 'Wargrave Pink'	Geraniaceae
Iris germanica L.	'Gold Galore'	Iridaceae
Iris germanica L.	'Immortality'	Iridaceae
Iris germanica L.	'Royal Touch'	Iridaceae
Paeonia lactiflora Pallas	Peony, 'Sarah Bernhardt'	Paeoniaceae
Paeonia lactiflora Pallas	Peony, 'Duchessee De Nemours'	Paeoniaceae
Paeonia lactiflora Pallas	Peony, 'Felix Crousse'	Paeoniaceae
Petunia × *hybrida* Vilm	Red hybrid petunia	Solanaceae
Petunia × *hybrida* Vilm	White hybrid petunia	Solanaceae
Petunia × *hybrida* Vilm	Yellow hybrid petunia	Solanaceae
Thalictrum aquilegifolium L.	Meadow rue	Ranunculaceae

there was one centrally located plot that was sprayed with sugar water, with four replicates of three additional plots at 3-, 9-, and 12-m distance from the central plot, extending in each of the four cardinal directions. Twenty third instars of *P. japonica* were placed on the surface of the turf in each enclosure, except for the central sugar-sprayed plots, and allowed to burrow into the ground. The central plot in each block was retreated with 150 ml of a 10% sugar water solution every 2 d. The sugar-sprayed plots were observed for a total of 30 min at ≈1100 hours on each of five dates, and numbers of *T. vernalis* landing and feeding on the treated turf were counted. After 14 d, all plots were excavated as described above and numbers of parasitized *P. japonica* were counted. Main effects of block and distance of grubs from the central sugar-sprayed plot were analyzed by two-way ANOVA followed by polynomial contrasts to test for linear effect of distance (Analytical Software 2000).

In spring 2002, the experimental layout was changed to increase the distance between the sugar-sprayed and unsprayed turf plots. In this set of experiments, 42 plots were created by implanting six parallel rows of seven PVC rings (39.0 cm in diameter by 10.2 cm in height) into the turf. The turf within the center ring in each row was sprayed with sugar water and the plots on opposite sides of the sugar-sprayed plot were positioned at 10, 30 and 50 m away. A minimum of 20 m was left between each row of plots. All other procedures for infesting the plots with grubs and for evaluating parasitism rates were the same as in the preceding year.

Similar experiments were conducted on parasitism of *Cyclocephala* spp. grubs by *T. pygidialis* in late summer. On 15 August 2001, 42 plots were created by implanting six parallel rows of seven PVC rings (39.0 cm in diameter by 10.2 cm in height) into a stand of Kentucky bluegrass turf at the University of Kentucky Spindletop Research Farm. In each row, the center plot was sprayed with sugar water, and the plots on opposite sides of the sugar-sprayed plot were positioned at 3, 9, and 12 m away. Twenty third instars of *Cyclocephala* spp. were introduced into each unsprayed plot as before. The experiment was repeated in August 2002 except that the distance between plots was increased to 10, 30, and 50 m from the sugar-sprayed central plot. Numbers of wasps visiting the plots were monitored as before. In both experiments, the plots were dug after 14 d and parasitism rate was determined and analyzed as described above.

Floral Visitation by *Tiphia* spp. A field study was conducted to determine whether stands of particular flowering plants might be used to attract *Tiphia* spp. If so, such plantings might be used to increase rates of parasitism of grubs in nearby turf. One garden consisting of spring-blooming perennials and annuals (Table 1), and two gardens comprised of fall-blooming perennial and annual flowers (Table 2), were established at the University of Kentucky Spindletop Research Farm. Flower species used in these gardens were recommended by S. Bale, (Department of Horticulture, University of Kentucky) based on compatibility with golf course landscapes and their perceived attractiveness to insects via nectar production. Gardens were established in a completely randomized design. Each plot measured 5 by 5 m and contained five plants of the same species. There were three replicate plots for each flower species. Each garden was monitored for 1 h between 1100 and 1400 hours, three times per week during the flight periods of *T. vernalis* (mid-April to early June) and *T. pygidialis* (mid-August to early October). Numbers of adult wasps and the plant species they were found on were recorded.

Effects of Peonies on Parasitism of *P. japonica*. Based on our observations (early spring 2003) of attraction of *T. vernalis* to peony, we examined whether incorporation of this plant species into a stand of turf might be a possible tactic for increasing parasitism of *P. japonica.* The study site for this experiment was a field of Kentucky bluegrass (120 by 80 m) at the University of Kentucky Spindletop Research Farm. Despite our previous observations of relatively low numbers of *T. vernalis* at this site in past years, this stand of turf was chosen because of its large size and lack of surrounding trees with honeydew that might attract *T. vernalis* and confound the results. On 5 May 2003, 40 plots were created by implanting five parallel rows of eight PVC rings (39.0 cm in diameter by 10.2 cm in height) into the turf. In the center of each

Table 2. Plant species established in the fall gardens and monitored for visits by fall active *Tiphia* spp.

Plant species	Common name	Family
Achillea millefolium L.	Yarrow	Asteraceae
Acinos arvensis Dandy	Basil thyme	Lamiaceae
Agastache foeniculum (Pursh) Kuntze	Anise hyssop	Lamiaceae
Asclepias tuberosa L.	Butterfly weed	Asclepiadaceae
Daucus carota L.	Queen Anne's lace	Apiaceae
Echinacea purpurea (L). Moench	Purple coneflower	Asteraceae
Exacum sp.	Exacum	Gentianaceae
Foeniculum vulgare Miller	Fennel	Apiaceae
Lobelia cardinalis L.	Cardinal flower	Campanulaceae
Lobelia siphilitica L.	Great blue lobelia	Campanulaceae
Melampodium paludosum L.	Medallion flower	Asteraceae
Nicotiana alata × *sanderae* Link and Otto	Flowering tobacco	Solanaceae
Rudbeckia hirta L.	'Irish Eyes'	Asteraceae
Rudbeckia hirta L.	'Rustic Colors'	Asteraceae
Rudbeckia ratibida L.	Prairie coneflower	Asteraceae
Salvia farinacea Bentham	Mealy-cup sage	Lamiaceae
Salvia uliginosa Bentham	Bog sage	Lamiaceae
Salvia viridis L.	Clary sage	Lamiaceae
Verbena canadensis (L.) Britton	'Aztec Mix'	Verbenaceae
Zinnia elegans Jacquin	Common zinnia	Asteraceae

row, a group of four peonies, each plant ≈1 m in height and having 8–10 blooms, was established with the plots on opposite sides of the plants positioned at 1, 10, 30, and 50 m away. Twenty third instars of *P. japonica* were introduced into each plot as before. On 2 June 2003, each plot was excavated, and numbers of parasitized and total *P. japonica* grubs were counted. Main effects of block and distance of grubs from the peonies were analyzed by two-way ANOVA (Analytical Software 2000).

Results

Effects of Sugar Water and Host Feeding on Wasp Longevity. Female *T. vernalis* and *T. pygidialis* with access to sugar water survived 4–6 times longer than those receiving only distilled water (Fig. 1; two-way ANOVA; $F = 181.96$; df = 1, 57; $P < 0.0001$ and $F = 138.41$, df = 1, 57; $P < 0.0001$, respectively). Presence of a grub for host feeding did not affect wasp longevity for *T. vernalis* ($F = 1.86$; df = 1, 57; $P = 0.18$) or *T. pygidialis* ($F = 1.38$; df = 1, 57; $P = 0.25$) nor was there significant interaction between sugar water and host presence on longevity for either wasp species (Fig. 1; $F = 2.02$; df = 1, 57; $P = 0.16$ and $F = 1.80$; df = 1, 57; $P > 0.19$, respectively).

Effects of Sugar Sprays on Grub Parasitism. Large numbers of *T. pygidialis* were found feeding on the sugar sprays applied to turf during experiments in all three years. Mean (±SE) number of *T. pygidialis* wasps observed on the six sugar-sprayed 0.12-m^2 turf plots during the 30-min inspections done during the 2000 tests were 4.3 ± 0.8, 6.3 ± 1.8, 6.5 ± 1.1, 13.0 ± 4.1, and 8.8 ± 3.8 on 15, 17, 19, 21, and 23 August 2000, respectively. No *T. pygidialis* were observed on the control plots during those periods. Surprisingly, there was a 4-fold decrease in *Cyclocephala* spp. grubs parasitized in sugar-treated plots compared with control plots (Fig. 2; paired *t*-test, $t = 3.81$, df = 11, $P = 0.003$).

In the experiment conducted in fall 2001, parasitism rates of *Cyclocephala* spp. grubs in plots at 3, 9, and 12 m from sugar-sprayed turf did not differ significantly ($F = 0.92$; df = 2, 14; $P = 0.44$). Mean (±SE) numbers of parasitized *Cyclocephala* spp. grubs per plot were 5.2 ± 1.8, 7.0 ± 3.0, and 2.6 ± 0.9 at 3, 9, and 12 m from the sugar water-sprayed turf, respectively. Mean (±SE) numbers of *T. pygidialis* wasps observed on the sugar-sprayed plots during the 30-min observation periods were 2.8 ± 0.9, 9.2 ± 2.1, 10.5 ± 2.6, 8.0 ± 2.7, and 3.7 ± 1.3 on 22, 24, 26, 28, and 30 August 2001, respectively. However, when the distance of plots from the sugar sprays was increased in 2002, the treatment effect was significant (Fig. 3; $F = 5.75$; df = 2, 35; $P < 0.05$), with a linear decrease in parasitism at

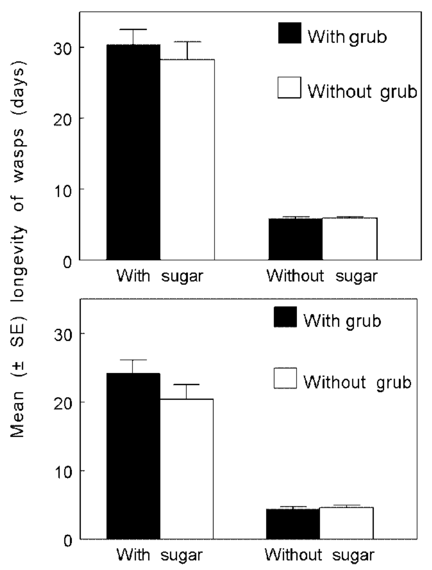

Fig. 1. Survival of wasps confined in laboratory at 22–24°C and a photoperiod of 14:10 (L:D) h with and without sugar water and host grubs. Top, survival of *T. vernalis*. Bottom, survival of *T. pygidialis*. Values are means (±SE) for 20 wasps per treatment.

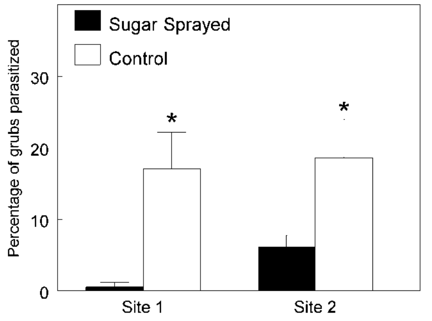

Fig. 2. Percentage of *Cyclocephala* spp. grubs parasitized by *T. pygidialis* in sugar-sprayed and unsprayed field plots. Plots (0.12 m^2) were established with 20 grubs each. Mean (±SE) number of total grubs recovered from sugar-sprayed versus control plots was 24.3 ± 1.0 versus 22.5 ± 1.4 at site 1, and 23.0 ± 2.1 versus 24.0 ± 1.8 at site 2. Means marked with an asterisk are significantly different than the control (paired *t*-test, $P < 0.05$).

increasingly greater distance from the sugar-sprayed turf (Fig. 3; polynomial contrasts; $F = 11.44$; df = 10; $P < 0.05$). Mean (±SE) numbers of *T. pygidialis* wasps observed in the sugar-sprayed enclosures during the 30-min inspections were 11.3 ± 1.9, 3.5 ± 0.9, 10.3 ± 2.5, 9.5 ± 2.1, and 7.8 ± 3.8 on 18, 20, 22, 24, and 26 August 2002, respectively.

During the spring experiments, no *T. vernalis* were observed visiting any of the sugar-sprayed turf plots. Sugar sprays applied to the foliage of oak trees growing ≈30 m away attracted hundreds of *T. vernalis*, confirming the wasps' presence in the area. In the spring experiments (2001 and 2002), there was no significant difference in parasitism of *P. japonica* grubs in any of the turf plots ($F = 0.85$; df = 2, 71; $P = 0.46$ and $F = 1.7$; df = 2, 35; $P = 0.23$, respectively). Mean (±SE) number of *P. japonica* grubs parasitized at 3, 9, and 12 m from the sugar sprays was 0.5 ± 0.2, 0.3 ± 0.2, and 0.33 ± 0.2, respectively. When the distance of the plots was increased to 10, 30, and 50 m from the sugar-sprayed turf, the mean (±SE) number of *P. japonica* grubs parasitized was 0.3 ± 0.2, 1.0 ± 0.6, and 1.7 ± 0.8, respectively.

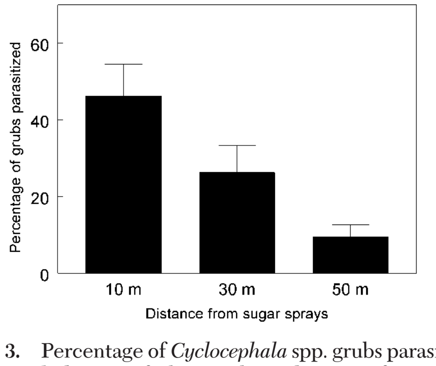

Fig. 3. Percentage of *Cyclocephala* spp. grubs parasitized by *T. pygidialis* in turf plots at three distances from sugar-sprayed turf. Plots were established with 20 grubs each. Mean (±SE) number of total grubs recovered from plots at 10, 30, and 50 m was 8.8 ± 1.5, 12.3 ± 1.2, and 14.7 ± 0.6, respectively.

Floral Visitation by *Tiphia* spp. No *T. pygidialis* wasps were observed visiting the gardens of fall-blooming plants during that species' flight period. Patches of turf within 30 m of the fall gardens sprayed with sugar water were visited by hundreds of *T. pygidialis.* Very few *T. vernalis* wasps were found visiting plants in the spring blooming garden. During 12 total hours of observations during May 2001 and 2002, only nine *T. vernalis* were found on any plants. The plants on which those wasps were observed included *P. lactiflora; Centaurea montana* L.; and German iris, *Iris germanica* L. 'Gold Galore'. Sugar sprays applied to the foliage of nearby trees were visited by many hundreds of *T. vernalis* within a short period. At the conclusion of these observations of the flower gardens in 2002, the gardens were plowed under. During spring 2003, one plant species, *P. lactiflora*, grew back in these plowed areas, with the plants larger, and with more blooms than in the preceding year. Despite our observations of low numbers of *T. vernalis* on these plants in the gardens during 2001 and 2002, numerous *T. vernalis* were found feeding on the extrafloral nectaries of the unopened blooms of these 30 reestablished plants during late April and May 2003. For example, the mean (±SE) numbers of *T. vernalis* wasps observed feeding on each *P. lactiflora* during 30-min observations were 7.6 ± 2.3, 13.1 ± 3.1, 10.8 ± 1.1, and 6.5 ± 0.3 on 2, 4, 7, and 9 May 2003, respectively.

Effects of Peonies on Parasitism of *P. japonica.* Parasitism of *P. japonica* was highest in the turf plots closest to the plantings of peonies (Fig. 4; $F = 14.3$; df = 3, 39; $P < 0.0001$). Mean (±SE) number of *T. vernalis* wasps observed feeding on *P. lactiflora* in each of the five plantings during 30-min inspections were 1.1 ± 0.6, 3.2 ± 1.3, 2.9 ± 1.6, and 2.3 ± 0.6 on 6, 8, 15, and 22 May 2003, respectively.

Discussion

Availability of nutrients is an important factor in the success of biological control agents (van Lenteren et al. 1987, Hagen et al. 1984). In the laboratory, longevity of *T. pygidialis* and *T. vernalis* provided with a carbohydrate source in the form of sugar water averaged 30 d, whereas wasps receiving only water lived an average of 6 d. Similar results have been documented for other hymenopteran parasitoids (Baggen and Gurr 1998, Jacob and Evans 2000, Gurr and Nicol 2000). Host feeding can also increase the longevity of parasitoids when supplemental sugar sources are also present (Heimpel and Collier 1996, Heimpel et al. 1997). In our study however, presence of a grub for host feeding did not affect wasp survival when sugar water was either provided or withheld. It is likely that host feeding by *Tiphia* serves only to mature eggs, which this study did not evaluate.

Carbohydrates, the main energy source for most insects (Hagen et al. 1984), may be obtained from floral nectars or honeydew produced by aphids and scale insects (Clausen et al. 1933, Baker and Baker

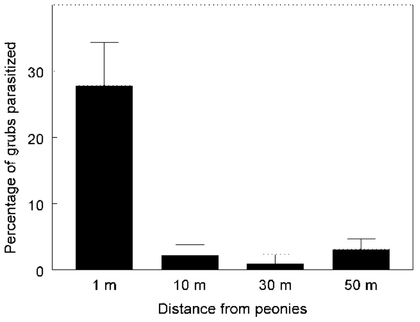

Fig. 4. Percentage of *P. japonica* grubs parasitized by *T. vernalis* in turf plots at four distances from peonies. Plots were established with 20 grubs each. Mean (±SE) number of total grubs recovered from plots at 1, 10, 30, and 50 m was 10.8 ± 0.9, 10.3 ± 0.9, 10.8 ± 1.3, and 11.0 ± 0.8, respectively.

1983, Hagen 1986, England and Evans 1997). When such food sources are unavailable, artificial food sprays have been used to enhance the effectiveness of natural enemies in the field (Hagen 1986, Jacob and Evans 1998). Hundreds of *T. pygidialis* were found feeding on our turfgrass plots sprayed with sugar water during August. Although there were no significant differences in parasitism of *Cyclocephala* spp. grubs at 3, 9, and 12 m from the sugar-sprayed turf in 2001, when distance of the plots containing grubs was increased to 10, 30, and 50 m from the sugar sprays in 2002, there was significantly higher parasitism closer to the food source. Direct application of sugar water to grub-infested turf; however, had the opposite effect. In the experiment with paired plots, one sugar sprayed and the other unsprayed, parasitism was significantly reduced in the turf sprayed with sugar water. Food availability and internal nutritional state can determine whether a parasitoid forages for hosts or food (Lewis et al. 1998). If wasps that came in contact with the sugar-treated turf were food-limited, feeding might have then taken precedence over burrowing into the soil and locating a host. Alternatively, reduced parasitism may be a result of sugar sprays masking the cues used by the wasps to locate patches of hosts. The result of this experiment illustrates the importance in understanding both the host- and food-foraging behavior of parasitoids when attempting to enhance biological control through addition of supplemental food sources.

Sugar sprays applied to turfgrass in the spring had no effect on parasitism of *P. japonica* by *T. vernalis.* This is not surprising because *T. vernalis* were never found feeding on the sugar-sprayed turf. The relatively low parasitism rate of *P. japonica* by *T. vernalis* in that experiment may have been due to the plots being several hundred meters from the nearest trees where the wasps were seen feeding on homopteran honeydew. Thus, it is likely that the females had to migrate some distance from their feeding sites to parasitize grubs in this field.

The difference in response to sugar sprays by *T. vernalis* and *T. pygidialis* is possibly explained by their feeding and mating habits. According to Clausen et al. (1932), spring-active *Tiphia* spp. feed primarily on homopteran honeydew, which is abundant early in the growing season on the foliage of trees. Indeed, we have frequently observed *T. vernalis* feeding on honeydew deposits from soft scales or aphids and have collected hundreds of the wasps by spraying sugar water on tree foliage (Rogers and Potter 2002a,b, 2003). Fall-active *Tiphia* spp., in contrast, have been assumed to feed mostly at plant nectaries or flower blossoms, rather than on homopteran honeydew, even when the latter is abundant (Clausen et al. 1932). The natural food source for adult *T. pygidialis* is presently unknown; however, we have not observed them to feed on sugar sprays applied to the foliage of trees. Also, *T. vernalis* mate on the foliage of trees, whereas *T. pygidialis* mate directly on the turf (M.E. R., unpublished data). Thus, some wasps observed feeding on the sugar sprays in those respective habitats likely were arrested by the food while searching for a mate. Hagen et al. (1971) demonstrated that predators (e.g., adult lacewings) were arrested, not attracted, by sucrose sprays alone and that addition of an attractant such as tryptophan to sucrose solutions was necessary to recruit them from a distance (Hagen et al. 1976).

Many studies (e.g., Foster and Ruesink 1984, Idris and Grafius 1995) have shown an increase in the longevity and fecundity of hymenopteran parasitoids fed on flowers. Despite past anecdotal reports of *Tiphia* visiting flowering plants (Clausen et al. 1927, Tooker and Hanks 2000), no *T. pygidialis* were found visiting fall-blooming plants in our gardens. These fall gardens contained flowering Queen Anne's lace, *Daucus carota* (L.), an umbelliferous plant often associated with fall-active *Tiphia* spp. in the older literature (Clausen et al. 1927, King and Holloway 1930). Only a few *T. vernalis* were found on three plant species in the garden comprised of spring blooming flowers in 2001 and 2002. The first, *P. lactiflora,* is touted in organic gardening literature as being attractive to *T. vernalis* because of its abundant extrafloral nectaries (Long 2000). The second species, *Centaurea montana* (mountain bluet), we observed to frequently be visited by ants, even when not in bloom. It probably also contains extrafloral nectaries. Attraction of a few *T. vernalis* to *Iris germanica* can likely be explained by the large yellow flowers it produces. We have found *T. vernalis* to be readily attracted to yellow-colored pan traps and sticky cards (Rogers and Potter 2002b). Coincident with the periods that these gardens were monitored, sugar sprays applied to adjacent turf or trees attracted hundreds of *T. pygidialis* and *T. vernalis,* respectively, confirming that both species were abundant and active in the area.

The reason that the peonies recruited many more *T. vernalis* in 2003 than in the previous 2 yr is unclear. One possibility may be that when incorporated into the garden with many other species of flowering plants, *P. lactiflora* was less apparent to foraging wasps. Also, unlike the annuals and other perennials that attained full size in the first growing season, the peony plants were relatively small in the first 2 yr, producing only one or two blooms, whereas the ones that reestablished in 2003 were taller and more robust, with 8–10 blooms per plant. Another possibility may be that during spring of the first 2 yr, other food sources (e.g., homopteran honeydew) were more readily available and preferred by *T. vernalis.* Consequently, it is possible that some of the other flowering plants we determined to be unattractive to *T. vernalis* and *T. pygidialis* might recruit some wasps if grown under different conditions.

Gardner (1938) observed that parasitism rates of *P. japonica* by *T. vernalis* were highest near trees with foliage covered with aphid honeydew. In our experiments with plantings of *P. lactiflora,* the first to manipulatively test this phenomenon, parasitism was increased from 1 to 3% in the open turf to ≈24% close to the peonies.

This study suggests that providing supplemental foods in the form of sugar sprays or certain nectar-producing plants has potential for enhancing parasitism of white grubs by *Tiphia* spp. by increasing the number of wasps feeding in an area. Such foods may also prolong wasp longevity in the field. This has implications not only for conserving native tiphiid populations (e.g., *T. pygidialis*) but also for introduction and establishment of wasps in new areas. Many species of *Tiphia* imported and released in the 1920–1940s for biological control of *P. japonica* failed to become established (Krombein 1948). Some of these failures were attributed to a lack of suitable food for adult wasps. Indeed, food availability may be the most important factor limiting the establishment and distribution of *Tiphia* spp. (Clausen et al. 1933, Gardner and Parker 1940). Establishment of *T. vernalis* in areas of the United States where *P. japonica* has spread is still being attempted (Smitley 2002). Applying supplemental food sprays to the foliage of trees in areas where *P. japonica* hosts are abundant may facilitate the establishment of these exotic parasitoids.

Perhaps a more sustainable approach for enhancing biocontrol of *P. japonica* in landscapes or on golf courses would be to incorporate woody plants harboring honeydew-producing homopterans in areas adjacent to turf. It is noteworthy that the golf course where most *T. vernalis* were collected for this study has fairways bordered by mature oaks (*Quercus* spp.), maples (*Acer* spp.), and other woody plants infested with aphids and soft scales. *T. vernalis* are more abundant at this site than at any of our more open (i.e., less wooded) golf course study sites, with parasitism of *P. japonica* as high as 50% (Rogers and Potter 2002b). Establishment or enhancement of *T. vernalis* populations might also be facilitated by provision of nectar-producing plants such as *P. lactiflora* into areas bordering lawns or golf courses. Longer term studies that incorporate such plants at multiple locations across a range of habitats are needed to fully evaluate the effectiveness of this tactic for biological control of white grubs.

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