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# Evaluation of corn leaf aphid (*Rhopalosiphum maidis*; Homoptera: Aphididae) honeydew as a food source for the egg parasitoid *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae)

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### Abstract

The effect of honeydew produced by the corn leaf aphid, *Rhopalosiphum maidis* (Homoptera: Aphididae), on the longevity and parasitism performance of the egg parasitoid *Trichogramma ostriniae* (Hymenoptera: Trichogrammatidae) was evaluated in a series of experiments conducted on corn (*Zea mays*) plants under controlled laboratory conditions. Wasps confined in bioassay cages on corn leaves with either honey or aphids survived on average 212.0 h and 206.7 h, respectively, which was significantly greater than the mean survival of wasps confined with only a corn leaf (29.1 h) or with nothing (28.5 h). To measure parasitism, wasp cohorts comprising one male and four females were confined on corn leaves either with or without aphids, and allowed to parasitize eggs of the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Crambidae). Wasps with access to aphid honeydew parasitized significantly more egg masses per day and a significantly higher proportion of eggs within each mass than wasps confined with only corn leaves. The total number of progeny produced by each wasp cohort per day and the proportion of progeny that were female were also significantly higher for the wasps provided with honeydew. Feeding treatment had no effect on the number of progeny emerging from each parasitized egg. We conclude that aphid honeydew has the potential to be an important within-field food resource that may impact the success of augmentative control of *O. nubilalis* by *T. ostriniae* released into cornfields.

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Keywords: Rhopalosiphum maidis; Trichogramma ostriniae; Ostrinia nubilalis; Zea mays; Parasitoid; Nonhost food; Aphid honeydew; Survival; Reproduction; Augmentative biological control

## 1. Introduction

Understanding the nutritional requirements of natural enemies of pests is essential to the design of maximally effective biological control strategies. While many parasitoids can obtain adult food requirements from their hosts, primarily through host feeding, a substantial proportion of species depend on food from nonhost sources (Lewis et al., 1998). Nonhost nutritional sources demonstrated to increase parasitoid survival and fecundity compared to unfed controls in laboratory studies include floral or extrafloral nectar (Lee et al., 2004; Shearer and Atanassov, 2004), pollen (Zhang et al., 2004), homopteran honeydew (Idoine and Ferro, 1988; England and Evans, 1997), honey (Hohmann et al., 1988; Leatemia et al., 1995), and various carbohydrate-only or carbohydrate-protein mixtures (Ashley and Gonzalez, 1974). In field studies, increased parasitoid numbers or increased parasitism of pest species have been reported for parasitoids provided access to nectar-producing plants, homopteran honeydew, or carbohydrate solutions sprayed onto crop plants (Powell, 1986; Treacy et al., 1987; Jacob and Evans, 1998). A lack of nonhost food resources for natural enemies has also long been recognized as a potentially important contributor to the failure of some biological control programs (Wolcott, 1942; Gurr and Wratten, 1999).

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Trichogramma Westwood wasps (Hymenoptera: Trichogrammatidae) are among the most widely used biological control agents, with augmentative releases of these minute egg parasitoids occurring on millions of hectares of agriculture and forest each year (Li, 1994; Smith, 1996). Romeis et al. (2005) have recently reviewed the use of different food sources by adult Trichogramma wasps. Although adults are known to host-feed (Blanche et al., 1996), female wasps provided with a carbohydrate source in addition to host eggs in laboratory studies generally exhibit much greater longevity and fecundity than wasps provided only host eggs (Leatemia et al., 1995; Olson and Andow, 1998; Shearer and Atanassov, 2004). In some Trichogramma species, newly emerged adult females have a strong food drive and will initially ignore host eggs in order to search for food (Hegazi et al., 2000). In a field study, Treacy et al. (1987) found higher rates of parasitism by T. pretiosum Riley on Heliothis zea (Boddie) (Lepidoptera: Noctuidae) eggs in cotton bearing extrafloral nectaries compared to cotton without nectaries. Similarly, buckwheat planted as a nectar-producing cover crop in vineyards improved the effectiveness of T. minutum Riley against grape berry moth (Endopiza viteana (Clemens); Tortricidae), resulting in lowered damage levels compared to fields with similar wasp release levels but without buckwheat (Nagarkatti et al., 2003). Lundgren et al. (2002), however, found no enhancement of T. brassicae Bezdenko performance against cruciferous Lepidoptera in cabbage plots with the use of weekly sugar sprays.

In this paper, we report on experiments assessing the potential of corn leaf aphid (*Rhopalosiphum maidis* Fitch; Homoptera: Aphididae) honeydew as a food resource for *Trichogramma ostriniae* Pang and Chen. *Rhopalosiphum maidis* is a common aphid species found in cornfields, and can cause crop damage and reduced yields through the removal of plant nutrients via sap-feeding, the vectoring of plant viruses, and the contamination of ears by the insects or by mold growing on the honeydew (Straub and Emmett, 1992; Bing, 1999). However, the species is considered only an occasional pest that is typically kept below economically injurious levels by natural enemies (Bing et al., 1999).

Trichogramma ostriniae was imported into the USA from China in the early 1990s for evaluation as an augmentative biological control agent against the European corn borer, Ostrinia nubilalis Hübner (Lepidoptera: Crambidae), which is a serious pest of corn (Zea mays L.) and other crops in North America (Mason et al., 1996). In field trials in the USA, the wasp species has shown considerable promise as an effective control agent against O. nubilalis in sweet corn (Wang et al., 1999; Hoffmann et al., 2002; Kuhar et al., 2002; Wright et al., 2002) as well as in solanaceous crops (Kuhar et al., 2004). Hoffmann et al. (1995) reported significant increases in longevity and fecundity for T. ostriniae females provided with continuous honey and O. nubilalis eggs in the laboratory, compared to wasps provided only with hosts. This suggests that other carbohydrate food resources, particularly ones such as aphid honeydew that

are likely to be naturally available in cornfields where *T. ostriniae* are released, could also improve wasp performance. The specific objectives of our study were to determine the effects of *R. maidis* honeydew on *T. ostriniae* longevity, parasitism rate, progeny production, and progeny sex ratio, under controlled laboratory conditions.

### 2. Materials and methods

### 2.1. Sources of organisms

The *T. ostriniae* used in the study were from a colony maintained on eggs of the Angoumois grain moth (*Sitotroga cerealella* (Olivier); Lepidoptera: Gelechiidae) by MPH at Cornell University, as described in Pitcher et al. (2002). *Rhopalosiphum maidis* adults and *O. nubilalis* egg masses were also obtained from laboratory colonies at Cornell. The aphids were maintained on barley, *Hordeum vulgare*, then transferred to corn 30 days prior to use in the study. All corn plants used in the study were sweet corn variety Silver Queen.

### 2.2. Bioassay cages

During the experiments, wasps and aphids were confined on corn plants in bioassay cages that consisted of 15–18 cm sections of dialysis tubing (48 mm diameter; VWR Scientific, San Francisco, CA) slipped over the fourth leaf of the corn plant and closed at both ends with foam stoppers. Each cage was also attached to stakes, which supported the cage's weight. All of the bioassays were performed in an environmental chamber under conditions of 16:8 (L:D) h, 25:22.7 °C (day:night), and 80% RH.

### 2.3. Effect of R. maidis honeydew on longevity of T. ostriniae

Nine replicate 38 cm diameter pots were planted with three corn plants per pot in late September 1999, and the corn plants reared in a greenhouse until the six-leaf stage, whereupon the pots were transferred to the environmental chamber. Each pot received four bioassay cages corresponding to the four different experimental treatments. For the honey treatment, three fine 1 cm long streaks of undiluted honey were applied to the interior of the cage with a fine paintbrush before the cage was attached to one of the corn plants in the pot. For the aphid treatment, the cage was attached to a corn leaf and then five adult R. maidis were introduced into the cage 24h prior to wasp introduction (within 24 h, honeydew was visible on the leaf). A third cage in each pot was assigned the leaf-only treatment and was attached to a corn leaf without receiving either honey or aphids. Finally, a fourth cage (nothing treatment) was placed in each pot without attaching it to a corn plant and without the addition of either aphids or honey.

Wasps were introduced into each cage by enclosing five parasitized (identified by their black color) *S. cerealella* eggs in a Pasteur pipette, waiting for the wasps to emerge from the host eggs, and then inserting the pipette into the cage to allow the wasps (all  $\leq 12$  h old) to move into the cage. This procedure avoided excessive handling of the wasps, which could have caused premature mortality. The number and sexes of the wasps entering each cage were noted to ensure that each cage had at least one male for the females to mate with. Beginning 6h after wasp introduction, and then every 12h thereafter, each cage was checked for the number of wasps remaining alive. Taking advantage of the positive phototaxis of Trichogramma wasps (Brower, 1991), wasp activity was checked by extinguishing the chamber lights and then attracting the wasps to a penlight placed atop each cage. When a wasp disappeared (no longer came to the light), it was assumed to have died midway between the time of the previous check and the time of the current check at which it disappeared.

For the analyses, each cage, rather than each individual wasp, was considered to be the replicate for which survival was measured, with the average of the survival times for all the wasps in a given cage taken as the survival time measure for that cage. This was done in order to meet the parametric assumptions of the statistical tests, and to permit sex ratio differences among cages to be taken into account in the survival analyses. Although most (22 of 36) cages had one male and four females, some cages had two males with 3-5 females. The longevity of male Trichogramma wasps is typically lower than that of females (Ashley and Gonzalez, 1974; Leatemia et al., 1995). Therefore, we analyzed the data using a general linear model (PROC MIXED, SAS version 9.1; SAS Institute, 2003) with Treatment as a categorical variable and the proportion of females in each cage cohort (PropFem) as a linear covariate, in order to account for any effects of wasp sex on survival times. The mean survival times per cage were also cube root transformed to meet the parametric assumptions of the general linear model. Pair-wise means comparisons were performed (LSMEANS statement within PROC MIXED), as appropriate, using the Bonferroni adjustment for multiple comparisons (family level of significance = 0.05).

# 2.4. Effect of R. maidis honeydew on parasitism and fecundity of T. ostriniae

Ten replicate pots were planted with two corn plants per pot, and the plants reared in the environmental chamber until the four-leaf stage, whereupon they were used for the experiments. Each pot had two bioassay cages, one attached to each corn plant and assigned either the aphid treatment or the leaf-only treatment, as described under the methods for the longevity experiment. All cages received four female and one male *T. ostriniae*.

Each day for nine days, a wax paper strip with eight closely clustered fresh (<24 h old) *O. nubilalis* egg masses was placed on the upper surface of the corn leaf in each cage and left for 24 h. To prevent wasp escape, the eggs were introduced and removed through a  $1 \times 1$  cm window that was cut into the cage tubing and covered with wax

paper. Prior to placement in the cages, the egg masses were dusted with *O. nubilalis* scales. Moth scales stimulate intensified searching and parasitism in many *Trichogramma* species, and *T. ostriniae* females are known to respond positively to *O. nubilalis* scale volatiles (Yong et al., 2006). Following exposure to wasps, the egg mass strips were incubated in 30 ml plastic cups sealed with paper lids to determine parasitism (indicated by blackening of parasitized eggs). Any emerged *O. nubilalis* larvae were removed to prevent cannibalism, and successfully emerged wasps were counted and sexed using antennal characters (Pinto, 1998).

The measures of T. ostriniae parasitism and fecundity that we examined were: the number of egg masses parasitized (out of eight possible per day), the proportion of eggs parasitized per parasitized egg mass, total progeny production (from all eight egg masses per day), progeny per parasitized egg, and the proportion of females in the progeny. We determined the effects of feeding treatment (*Treatment*) and day of parasitism (Day) on these measures of performance (each dependent variable analyzed separately) using a repeated measures ANOVA (REPEATED statement within PROC MIXED, SAS version 9.1; SAS Institute, 2003) in which the wasp cohort within each bioassay cage was treated as a unique subject for which the dependent variable was measured repeatedly over multiple days. Only data for the first three days of parasitism were included in these analyses, because no parasitism occurred in the leafonly treatment after day 3. When necessary, transformations on the dependent variable were used to meet the assumptions of ANOVA. For each dependent variable, results are presented for the model that included Treatment and Day as main effects, as well as the interaction *Treatment*  $\times$  *Day* if this was significant at *P* < 0.05.

#### 3. Results

### 3.1. Effect of R. maidis honeydew on longevity of T. ostriniae

Feeding treatment had a highly significant effect on wasp longevity (F=656.7, df=3,31, P < 0.0001). Mean survival times in the honey (212.0±4.7 [sem] h) and aphid (206.7±8.5 h) treatments were more than 6× the mean survival times in the leaf-only (29.1±1.4 h) and nothing (28.5±1.4 h) treatments. Survival did not differ significantly between the honey and aphid treatments, nor between the leaf-only and nothing treatments (P > 0.2 for each comparison), however. The proportion of females in a cage also had no significant effect on the mean survival time per cage (F=0.94, df=1,31, P=0.3397).

# 3.2. Effect of R. maidis honeydew on parasitism and fecundity of T. ostriniae

Wasps given access to *R. maidis* honeydew parasitized significantly more egg masses each day (F=258.1, df=1,25.6, P < 0.0001) and a significantly higher proportion of eggs within each parasitized mass (F=174.5,



Fig. 1. Number of *O. nubilalis* egg masses parasitized per day (mean  $\pm$  SEM) and proportion of eggs parasitized per parasitized egg mass (mean  $\pm$  SEM), for *T. ostriniae* wasp cohorts confined on corn plants for nine days with or without *R. maidis* aphids (A, aphid treatment; L, leaf-only treatment). No parasitism occurred in the leaf-only treatment after day 3.

df = 1,23.7, P < 0.0001) than wasps given access only to corn leaves (Fig. 1). Day of parasitism also had a significant effect on both of these measures (F = 55.8, df = 2,38.1, P < 0.0001 for number of masses parasitized; F = 53.8, df = 2,37.1, P < 0.0001 for proportion of eggs parasitized per mass), with mean performance consistently decreasing over time regardless of feeding treatment (Fig. 1). The proportion of eggs parasitized per egg mass tended to decrease over time more rapidly in the aphid treatment than in the leaf-only treatment, however, resulting in a significant interaction between feeding treatment and day of parasitism for this performance measure (F = 10.4, df = 2,37.1, P = 0.0003).

Both feeding treatment and day of parasitism also had significant effects on the total number of progeny that successfully emerged from the eggs parasitized on a given day (F = 966.1, df = 1, 15.6, P < 0.0001 for effect of *Treatment*; F = 467.1, df = 2,31.2, P < 0.0001 for effect of Day; Fig. 2). The difference in mean progeny production between the two feeding treatments was much greater on day 1 than on day 3, however, resulting in a significant interaction term between *Treatment* and *Day* (F=152.8, df=2,31.2,P < 0.0001). Neither feeding treatment nor day of parasitism had a significant effect on the number of progeny produced per parasitized egg (F = 1.69, df = 1, 19.5, P = 0.2090for effect of *Treatment*; F = 1.30, df = 2,35.9, P = 0.2843 for effect of Day), however, at least for the first three days of the study (Fig. 2). Lastly, feeding treatment had a relatively small but significant effect on the proportion of progeny that were female (F = 7.55, df = 1,20.8, P = 0.0121; dependent variable arcsin transformed), with wasps in the aphid treatment producing more females (Fig. 3). This proportion stayed relatively constant over the first three days of parasitism, however, leading to a non-significant effect of time (F=1.44, df=2, 34.2, P=0.2566; dependent variable arcsintransformed).



Fig. 2. The total number of progeny produced per day (based on successful adult emergence after incubation) (mean  $\pm$  SEM) and the number of progeny produced per parasitized egg (mean  $\pm$  SEM), for *T. ostriniae* wasp cohorts confined on corn plants for nine days with or without *R. maidis* aphids (A, aphid treatment; L, leaf-only treatment). No parasitism occurred in the leaf-only treatment after day 3.



Fig. 3. The proportion of female progeny produced per day (based on successful adult emergence after incubation) (mean  $\pm$  SEM), for *T. ostriniae* wasp cohorts confined on corn plants for nine days with or without *R. maidis* aphids. No parasitism occurred in the leaf-only treatment after day 3.

### 4. Discussion

The results of our experiments demonstrate that *R. maidis* honeydew is a suitable food resource for *T. ostriniae* that can greatly increase wasp longevity and reproduction relative to no-food controls. McDougall and Mills (1997) similarly found increased survival of *T. platneri* Nagarkatti wasps provided with rosy apple aphid (*Dysaphis plantaginea* Passerini) honeydew, compared to water-only controls. Interestingly, McDougall and Mills (1997), who measured wasp longevity based on the mean survival of mixed-sex cohorts, as we did, found poorer survival of wasps fed honeydew compared to wasps fed undiluted honey, whereas we found comparable survival between wasps fed honeydew versus honey. McDougall and Mills (1997) note that their honeydew samples, which were collected from the field, likely had some fungal contamination that could have affected the honeydew's suitability as a food for *T. platneri*. Studies with hymenopteran parasitoids other than *Trichogramma* suggest that honeydew may often be an inferior food compared to other sugar sources such as floral nectar, though honeydew can still be beneficial relative to no-food controls (Wäckers, 2000; Lee et al., 2004). More studies with additional species are needed, however, to determine the extent to which *Trichogramma* wasps exhibit a pattern similar to other hymenopteran parasitoids in their responses to honeydew versus other carbohydrate sources.

To our knowledge, our study is the first to examine the effects of aphid honeydew on parasitism by Trichogramma wasps. Hoffmann et al. (1995) found that approximately one-third of female T. ostriniae deprived of food failed to parasitize any host eggs during their lifetimes, whereas 100% of females provided honey for the first 24h or longer parasitized at least some eggs. Most parasitoid wasps, including Trichogramma, have a mixed pro-/syn-ovigenic strategy, in which adult females eclose with a complement of fully matured eggs, but can also mature additional eggs if suitable food resources are available (Olson and Andow, 1998; Jervis et al., 2001). The lack of parasitism by unfed T. ostriniae females observed by Hoffmann et al. (1995) thus seems unlikely to be explained by egg limitation, and suggests that adult feeding shortly after eclosion can directly facilitate the host searching and parasitism behavior of T. ostriniae females. Such facilitation of Trichogramma searching and parasitism behavior by adult feeding has previously been documented by Hegazi et al. (2000) for T. cacoeciae, and can likely explain, in part, the differences in parasitism performance that we observed between wasps in the aphid and leaf-only treatments. This is particularly likely to be true for day 1 of the parasitism experiment, when we would have expected most of the wasps in each cage cohort to still be alive (based on the results of the longevity experiment) and to have a sizable complement of mature eggs available for oviposition. On days 2-3 of the parasitism experiment, death of some wasps in the leaf-only cohorts, and possibly egg limitation for leaf-only wasps unable to mature additional eggs, likely were additional factors contributing to the lower parasitism observed for the leaf-only treatment relative to the aphid treatment.

Wasp age effects, cumulative wasp mortality over time (particularly in the leaf-only treatment), and possibly egg limitation, were likely the main factors responsible for the declines, over time, in egg mass parasitism, proportion of eggs parasitized, and total progeny production that we observed. Hoffmann et al. (1995) recorded declines in fecundity, percent parasitism, percent progeny emergence, and percent female progeny, with increasing wasp age, for individual female *T. ostriniae* living up to 17 days when provided with continuous honey. The specific factors (*viz.*, wasp age, mortality, or egg limitation) responsible for the steeper decline over time in proportion of eggs parasitized and total progeny production for wasps in the aphid treatment compared to wasps in the leaf-only treatment (resulting in significant *Treatment* × *Day* interactions) cannot be

determined from our experimental design. Nevertheless, the consequence of this result is that parasitism performance was more similar between the two treatments on day 3 than on day 1. Further, although parasitism continued in the aphid treatment for up to 9 days, the amount of parasitism that occurred on days 4–9 was relatively low (presumably also due to effects of wasp age and/or egg limitation). Thus, even though access to honeydew allows wasps to greatly increase their longevity and therefore increase their reproductive lifespan, our results suggest that feeding on aphid honeydew will most likely have its greatest impact on *T. ostriniae* parasitism and ability to reduce pest numbers in the field during the first 1–2 days of life.

In central New York, where most of the research trials with T. ostriniae in the USA have been conducted, R. maidis and R. padi colonies on corn plants, as well as other aphids on weeds, are among the most abundant nonhost carbohydrate sources available to Trichogramma and other parasitoids in or near cornfields (JRF, unpublished). We have also observed T. ostriniae readily imbibing nectar from buckwheat (Fagopyrum esculentum; Polygonaceae) flowers and a variety of other flower species in the laboratory (MPH, unpublished), which suggests that the wasps would be able to obtain nectar from many of the flowering plants commonly found in or near New York cornfields, such as Pennsylvania smartweed (Polygonum pennsylvanicum; Polygonaceae) and common milkweed (Asclepias syriaca; Asclepiadaceae) (JRF, unpublished). Zhang et al.'s (2004) finding that corn pollen can serve as a food source for T. brassicae adults in the laboratory suggests that T. ostriniae could potentially utilize corn pollen as a food resource in the field as well.

Aphid honeydew seems likely to be the nonhost food most commonly encountered and utilized by T. ostriniae wasps released against O. nubilalis in cornfields, however, because corn pollen is available during only brief periods, and many nectar resources would require wasps to travel long distances from within the cornfield to field margins or other areas where aggregations of weedy flowering plants are found. Compared to other parasitoid species, a large travel distance to find food could be particularly prohibitive for Trichogramma wasps, because of their small size, short lifespan, and relatively poor flying ability (Keller et al., 1985). Sources of honeydew such as R. maidis aggregations, on the other hand, could potentially be located on the very same corn plants where T. ostriniae wasps are searching for O. nubilalis host eggs. Feeding on corn aphid honeydew could thus provide wasps with a valuable nutritional benefit while incurring little cost in terms of time and energy diverted from reproduction in order to search for food (Lewis et al., 1998). Hungry parasitoids may also simply abandon plant patches lacking food, even when hosts are available (Lewis et al., 1998). Thus, a within-field food resource such as R. maidis honeydew could improve T. ostriniae efficacy by increasing wasp retention in the cornfields where they are released, as well as by serving as a source of nutrition that can increase wasp longevity and reproduction.

To our knowledge, there have been no published studies specifically examining the effect of aphid or honeydew presence on the biocontrol efficacy of Trichogramma wasps under field conditions. However, Trichogramma performance against pests in cotton and vineyards were improved by the presence of cotton extrafloral nectar (Treacy et al., 1987) and floral nectar from interplanted buckwheat (Nagarkatti et al., 2003), respectively, which suggests that other within-field carbohydrate sources such as aphid honeydew could also promote increased parasitism and improved pest control by Trichogramma. An effect of aphid presence on parasitoid efficacy in the field was found by Jacob and Evans (1998) for Bathyplectes curculionis (Hymenoptera: Ichneumonidae), a parasitoid of alfalfa weevil (Hypera postica; Coleoptera: Curculionidae). These authors found increased B. curculionis densities in alfalfa fields in response to increases in pea aphid (Acyrthosiphon pisum; Homoptera: Aphididae) densities, as well as increased wasp densities and increased weevil parasitism in fields receiving sugar sprays, which were intended to mimic the presence of honeydew.

In conclusion, there are several lines of evidence that suggest that R. maidis presence may impact the overall success of field suppression of O. nubilalis with T. ostriniae. Aphid honeydew is likely to be one of very few carbohydrate sources available to T. ostriniae in or near cornfields. In laboratory studies, R. maidis honeydew enhances T. ostriniae parasitism of O. nubilalis eggs. Aphid colonies are also likely the only sugar source located directly on corn plants, minimizing the need for wasps to travel between host and food patches, and increasing wasp retention in release fields. Nonhost foods may be particularly important with early season inoculative releases of T. ostriniae against O. nubilalis (Hoffmann et al., 2002), when increased wasp longevity and reproduction can help ensure wasp population maintenance and buildup during periods when O. nubilalis egg abundance may be relatively low. In the future, considering the availability in or near cornfields of aphid honeydew and other nonhost foods for T. ostriniae may allow us to improve our ability to manipulate wasp releases against O. nubilalis for increased efficiency and profit.

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