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Biological Control

Growth, development and consumption by four syrphid species associated with the lettuce aphid, *Nasonovia ribisnigri*, in California

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ABSTRACT

The lettuce aphid, *Nasonovia ribisnigri* Mosley, was accidentally introduced into California from Europe during the late 1990s and soon became an economic pest of Romaine lettuce along California's central coast region. Indigenous syrphid larvae attack the lettuce aphid and are believed to be effective in the management of this invasive pest, although there have been no studies on the capacity of the syrphid larvae to kill and consume lettuce aphids. We focused on four syrphid species commonly found in central coast lettuce fields: *Allograpta obliqua* (Say), *Eupeodes fumipennis* (Thomson), *Sphaerophoria sulphuripes* (Thomson), and *Toxomerus marginatus* (Say). Laboratory feeding experiments were conducted to estimate the development times of all juvenile stages, the daily growth rate of larvae, the number of third instar aphids killed, the aphid biomass killed, and the aphid biomass consumed as measures of predator performance. Results show that during larval development *E. fumipennis* killed the most third-instar aphids (507 aphids, 88 mg biomass killed) and reached the largest size, followed by *A. obliqua* (228 aphids, 39 mg killed), *S. sulphuripes* (194 aphids, 31 mg killed) and *T. marginatus* (132 aphids, 20 mg killed). Body size alone did not account for species differences in per-capita larval consumption rates. This information is discussed in relation to the predation potential of syrphids through the short cropping cycle of lettuce, and the choice of plant species to use for floral resource provisioning to enhance the activity of syrphids needed for effective management of lettuce aphids in California's central coast fields.

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1. Introduction

The lettuce aphid, *Nasonovia ribisnigri* Mosley, was accidentally introduced into California from Europe during the late 1990s and has become an important pest of Romaine lettuce. *Nasonovia ribisnigri* can be difficult to control as it is characterized by rapid dispersal and colonization of the innermost leaves of the lettuce head (Parker et al., 2002), which provide a refuge from many natural enemy species. Although insecticide application(s) has been a standard management practice for *N. ribisnigri* (Natwick et al., 2008), it has not always been effective due to poor accessibility of aphids within the head of the lettuce and the development of insecticide resistance (Parker et al., 2002). For these reasons, the potential to utilize natural enemies more effectively has become of increasing interest in the management of the lettuce aphid. In California, a number of indigenous natural enemy species have found this invasive aphid to be a suitable new resource and, for this reason, have attracted attention for their potential role in lettuce aphid biological control.

Syrphid larvae are an important group of aphid natural enemies (Brewer and Elliott, 2004; Freier et al., 2007; Haenke et al., 2009; Tenhumberg and Poehling, 1995; Winder et al., 1994) and several field studies have demonstrated a direct relationship between syrphid egg and larvae densities and reductions in aphid densities in agricultural crops (Freier et al., 2007; Smith et al., 2008; Tenhumberg and Poehling, 1995). Syrphid flies are also commonly associated with the lettuce aphid along the central coast of California (Smith and Chaney, 2007). However, many field-level conditions in the lettuce crop influence the level of aphid suppression provided by natural enemies. For example, if natural enemies fail to colonize and suppress the aphid colonies early in the Romaine lettuce growth cycle, the plant growth can enclose the aphids, providing the pest some protection from natural enemies (Bugg et al., 2008).

California's organic lettuce growers have used floral resources to increase numbers of syrphid larvae in their fields (Bugg et al., 2008; Chaney, 1998; Smith et al., 2008). Whereas syrphid larvae depend on the consumption of aphids for growth and survival, adult syrphids rely on aphid honeydew and/or floral nectar and pollen for energy and egg production (Smith et al., 2008). Floral resources are well known to be beneficial in attracting predators and parasitoids to agroecosystems (Gurr et al., 2004; Landis et al., 2005; Robinson et al., 2008; Wackers and Van Rijn, 2005). Flower

color, morphology, size, odor, nectar and pollen load, age, remnants of previous visitors, or interactions with other pollinators or predators, can all influence which syrphid species visit a floral resource (Ambrosino et al., 2006; Colley and Luna, 2000; Haslett, 1989; Sutherland et al., 1999). The most common insectary plant currently used in lettuce fields is sweet alyssum (Lobularia maritima (L.) Desv.) (Smith and Chaney, 2007).

The use of floral resources to enhance syrphid activity, through conservation biological control, is based on the assumption that these natural enemies will respond at a sufficient level of abundance and per capita predation to suppress the aphid population and lessen crop damage. While it is known that insectary plantings do attract a greater abundance of adult syrphids in lettuce fields in California (Smith et al., 2008), the species attracted vary considerably in size, and their per capita capacity for predation of the lettuce aphid remains unknown. The importance of per capita capacity for predation is well illustrated from a study of syrphid predators of Aphis fabae Scopoli in which different species varied considerably in their larval consumption rates (Sood et al., 2007). In addition, other studies have demonstrated a positive relationship between larval body size and prey consumption for syrphid species (Hagvar, 1974; Tinkeu and Hance, 1998).

The goal of this study was to quantify the growth, development and larval consumption rates of syrphid larvae under laboratory conditions as an important step toward understanding the potential of different syrphid species to control populations of N. ribisnigri in lettuce fields in California. A variety of approaches can be used to estimate the per capita larval consumption rates of predators, either in the laboratory or in the field (Mills, 1997, 2005), and both methodology and choice of measurement variable (number or biomass of prey killed or consumed) can influence the estimates obtained (Latham and Mills, 2009). While it is often best to estimate the consumption rate of predators through direct field observation (Costamagna and Landis, 2007; Latham and Mills, 2010), this is less practical for syrphid larvae as they are commonly nocturnal in their activity. Here, we focused on four of the more common syrphid species found in California's central coast lettuce fields: Allograpta obliqua (Say), Eupeodes fumipennis (Thomson), Sphaerophoria sulphuripes (Thomson), and Toxomerus marginatus (Say). We estimated the development times of all juvenile stages, the daily growth rate of larvae, the number of aphids killed, and the aphid biomass consumed and killed. As these syrphid species differed considerably in adult body size, we hypothesized that the per capita consumption of lettuce aphids by syrphid larvae would be a function of predator size alone, with no significant variation in the consumption capacity per unit biomass among the four syrphid species.

2. Materials and methods

2.1. Experimental insects

The lettuce aphids used in all studies were from a laboratory colony established from individuals collected from Hollister, CA and reared on Romaine sunbelt lettuce (Lactuca sativa L.) at 20 °C and 16:8 h L:D photoperiod. The aphids were reared as cohorts by moving reproductive adults with a fine paintbrush every two days, and placing these adults in clear polypropylene containers (355 ml Pro-Kal®, Kalamazoo, MI). The containers were lined with moist filter paper, provisioned with fresh excised lettuce leaves, and closed with ventilated polypropylene lids (8.0 mm² area of polyester mesh). After removal of the reproductive adults, aphid nymphs were provided with fresh lettuce leaves every two days until used as prey for syrphid larvae. The majority of the nymphs used in the consumption study were in the third instar, based on life-table data at 20 °C (Diaz and Fereres, 2005).

We collected gravid female A. obliqua, E. fumipennis, S. sulphuripes and T. marginatus from two locations in California: Hollister and Berkeley. Field-collected syrphid females were placed individually in clear polypropylene oviposition containers (947 ml Pro-Kal®) with a ventilated polypropylene lid (8.0 mm² polyester mesh). Each container was provisioned with diluted honey (0.01% sorbic acid, 10% honey, 89.99% water) in a small cotton-wool stoppered plastic cup (22.2 ml SOLO®, Highland Park, IL), and a lettuce leaf with 10 N. ribisnigri of mixed instars that remained alive during the syrphid oviposition period (1–4 days). Eggs from the oviposition cages were collected daily and used for observations on development, larval growth and consumption of the four syrphid species, using eggs from different females whenever possible. Ovipositing female syrphids were subsequently frozen and used as vouchers to verify the identity of each species.

2.2. Syrphid development, larval growth and consumption

All life stages of each syrphid species were maintained at 19.3 °C (±0.6 SD) and a 16:8 h L:D photoperiod approximating average mid summer conditions in Hollister lettuce fields. Newly laid eggs were placed in separate plastic Petri dishes (3.5 × 1.0 cm), provided with a fresh disk of lettuce (3.2 cm diameter) and several aphids each day, and monitored every 24 h until hatching. After hatching, larvae were left undisturbed for 24 h as they were too fragile to be handled experimentally. Subsequently, individual larvae were provided with a fresh disk of lettuce, and a new set of aphids each day until they completed their larval development. Sample sizes of individuals that completed development to pupation were 17 for A. obliqua, 15 for E. fumipennis, 11 for S. sulphuripes, and 8 for T. marginatus. All individuals were checked daily until adult emergence to provide estimates of development time for each life stage, and fresh weight was measured daily (Sartorius 1801 microbalance with an accuracy of ±0.1 mg) to estimate larval growth rates.

Larval consumption was monitored for syrphid larval ages of days, 2, 3, 5, 7, and then every other day thereafter until pupation. On monitoring days we counted (with occasional exceptions) and weighed live aphids before and after exposure to the syrphid larvae, and counted and weighed dead and partially consumed aphids after exposure. On days 2 and 3; we gave larvae of all syrphid species 20 and 25 third instar aphid nymphs, respectively, and on subsequent monitoring days, the numbers of aphids given to larvae were always in excess, but varied with larval size. As a control, Petri dishes with aphids only were used to correct for non-predation aphid mortality and for the increase in fresh weight of aphids over the 24 h monitoring period. The mean fresh weight of the third instar lettuce aphids used was 0.13 mg (±0.04 SD, $n = 91$) and the fresh weight gain per live aphid was estimated from the control as ((final fresh weight of aphids/final number of aphids) − (initial fresh weight of aphids/initial number of aphids)). The correction for weight gain per aphid proved to be important as it averaged 0.04 mg (±0.03 SD, $n = 91$). We also estimated non-predation mortality of aphids as ((number of dead aphids/initial number of aphids) × 100). We found a 16.35% (±10.27% SD, $n = 91$) mortality rate of aphids over the 24 h period.

From these measurements we were able to estimate the daily number of aphids killed, biomass of aphids killed, and biomass of aphids consumed for the larvae of each syrphid species in relation to age on each monitoring day. As noted above, occasionally the number of aphids killed was not recorded on monitoring days, and in these cases it was estimated from the daily biomass killed divided by 0.15 mg, the mean corrected fresh weight of a third instar aphid at the mid point of a 24 h observation period. To correct the daily number of aphids killed for natural aphid mortality in the control (16.35%) the observed and estimated numbers killed were

multiplied by 0.8365. Assuming that consumption events by syrphid larvae were also regularly distributed around the mid-point of a 24 h monitoring period, and thus that consumed aphids would have gained half the daily mean weight gain, we corrected the daily estimates of biomass consumed (mg) to account for both the weight gain per aphid and the natural aphid mortality in Petridishes as follows. The corrections were obtained from ((initial fresh weight of live aphids – final fresh weight of live aphids) – (mean aphid weight gain × number of live aphids)) – ((final fresh weight of dead aphids) + (mean aphid weight gain × 0.5 × number of aphids consumed)). The daily biomass (mg) of aphids killed was corrected similarly, but in this case the final fresh weight of dead aphids was multiplied by 0.1635, the proportion of aphids that died naturally in the control Petri dishes.

On non-monitoring days, all syrphid larvae were provisioned with a sufficient, but not an excess, number of aphids to satisfy their requirements. All aphids that were provided were killed on the non-monitoring days, and while the number of aphids was noted their biomass was not measured. Thus for non-monitoring days the daily biomass of aphids killed was estimated from (number of aphids provided × 0.15 mg).

To estimate lifetime number of aphids killed and lifetime aphid biomass killed for each syrphid species we summed the corrected daily estimates for both monitoring and non-monitoring days over their entire larval period.

2.3. Data analysis

The data were analyzed with 'R' version 2.10.1 (R Development Core Team, 2009). Development times estimated for egg, larval and pupal stages were compared among the four syrphid species by ANOVA using the generalized linear hypothesis test (glht) with multiple comparisons of means (Tukey contrast) in the R package 'multcomp' (Hothorn et al., 2008). For larval growth in relation to age we fitted sigmoid curves of the form $y = a/(1 + \exp(-b(x - c)))$ for each syrphid species using the nonlinear least squares (nls) function in R, with significant differences among species for each of the fitted parameters assessed by 95% CI.

The daily number of aphids killed on monitoring days was compared among syrphid species in relation to larval age using 95% CI for those ages that included at least three replicates. A generalized linear model was used to analyze the daily aphid biomass killed in relation to syrphid species and larval fresh weight, using an identity link function, with 1 added to the estimated biomass killed, and a quasi error distribution with the variance set to the mean to avoid over dispersion. To determine which syrphid species differed significantly in daily biomass killed in relation to larval fresh weight, we specified species contrasts by aggregating non-significant factor levels in a stepwise a posteriori procedure (Crawley, 2007).

A paired Wilcoxon sum rank test was used to compare the cumulative aphid biomass killed and consumed on monitoring days over the larval period of each syrphid species. In addition, ANOVA (glht with Tukey contrasts in the R package 'multcomp' (Hothorn et al., 2008)) was used to test for differences among the four syrphid species in the lifetime number of aphids killed and biomass killed during the larval period.

3. Results

3.1. Syrphid development

Development times for each life stage and for the complete juvenile development period from oviposition to adult emergence were compared among the four syrphid species (Fig. 1). The mean
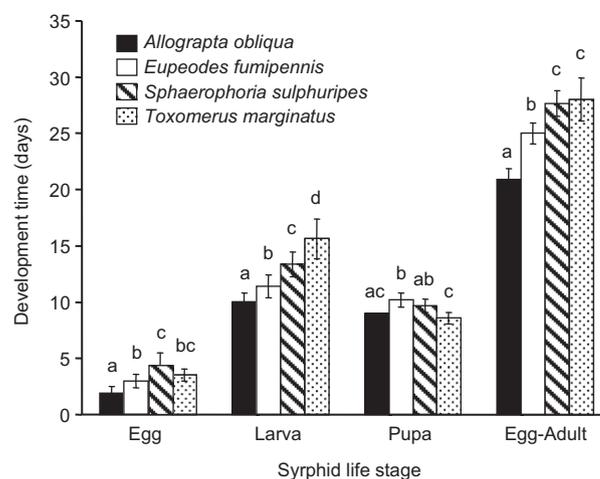

Fig. 1. Mean (±SD) duration of development for each life stage of *Allograpta obliqua*, *Eupeodes fumipennis*, *Sphaerophoria sulphuripes* and *Toxomerus marginatus* at 19.33 °C (±0.62 SD) and a 16:8 h L:D photoperiod. Bars with different letters are significant different among syrphid species within that life stage ($P < 0.05$).

time spent in the egg stage ranged 2–5 days, and varied significantly among syrphid species (ANOVA: $F = 72.12$, df = 3,49, $P < 0.001$), with *A. obliqua* development time significantly shorter than for the other three species ($P = 0.001$) and *E. fumipennis* having a shorter egg stage than *S. sulphuripes* ($P = 0.001$). The mean time spent in the larval stage ranged 10–16 days and also differed for all four syrphid species (ANOVA: $F = 53.69$, df = 3,49, $P < 0.001$), with development times increasing from *A. obliqua* to *T. marginatus* ($P < 0.004$). There were also differences in pupal development, which ranged 9–10 days (ANOVA: $F = 24.36$, df = 3,32, $P < 0.001$), with *E. fumipennis* pupal development longer than for *A. obliqua* and *T. marginatus* ($P < 0.001$), and *T. marginatus* shorter than for *S. sulphuripes* ($P < 0.004$). The complete juvenile development from egg to adult emergence ranged 21–28 days, and was significantly shorter for *A. obliqua* than for the other three species while *E. fumipennis* had a shorter development time from egg to adult emergence than *T. marginatus* and *S. sulphuripes* (ANOVA: $F = 73.21$, df = 3,32, $P < 0.001$ and Tukey contrasts, $P < 0.001$ for all pairwise combinations).

3.2. Syrphid growth

Daily growth in fresh weight followed a sigmoid pattern for all four syrphid species (Fig. 2). The asymptote (a), representing final larval fresh weight, was significantly different for all four species with that of the largest species *E. fumipennis* being almost five times larger than that for the smallest species *T. marginatus*. The rate parameter (b) for larval growth did not differ significantly between syrphid species. The inflection point (c), representing the age at the mid point of larval growth, was significantly later for *T. marginatus* than for *A. obliqua* or *E. fumipennis*, while that for *S. sulphuripes* did not differ from any other species.

3.3. Aphid numbers and biomass

The daily number of aphids killed by each of the four syrphid species was compared in relation to larval age, measured in days (Fig. 3). Based on non-overlap of 95% CI, the number of aphids killed did not differ among species at age 3, and *A. obliqua* and *E. fumipennis* differed significantly from each other only at age 10. *A. obliqua* and *E. fumipennis* both killed significantly more aphids than *T. marginatus* from ages 4 to 10, and significantly more than *S. sulphuripes* from ages 4 to 8. The number of aphids killed by *S.*
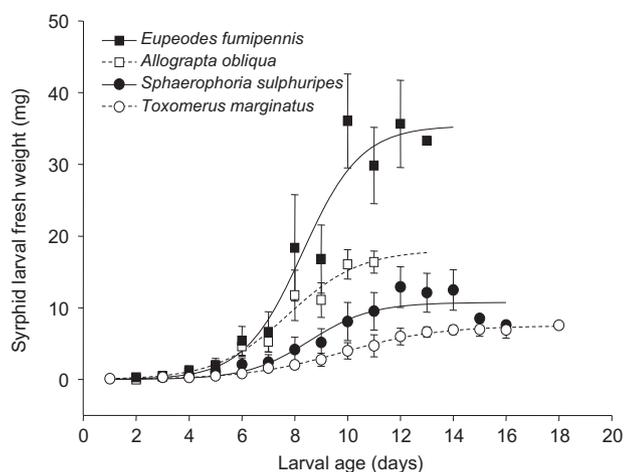
Fig. 2. Larval growth of *Allograpta obliqua*, *Eupeodes fumipennis*, *Sphaerophoria sulphuripes* and *Toxomerus marginatus* at 19.33 °C (±0.62 SD) and a 16:8 h L:D photoperiod. Growth curves of the form $y = a/(1 + \exp(−b(x − c)))$ were fitted for each species: *E. fumipennis* $a = 36.51^A$, $b = 0.82$, $c = 8.49^A$; *A. obliqua* $a = 20.04^B$, $b = 0.64$, $c = 8.28^A$; *S. sulphuripes* $a = 12.96^C$, $b = 0.68$, $c = 9.22^{AB}$; *T. marginatus* $a = 7.49^D$, $b = 0.55$, $c = 9.77^B$. Fitted parameters followed by different letters are significantly different among syrphid species ($P < 0.05$).
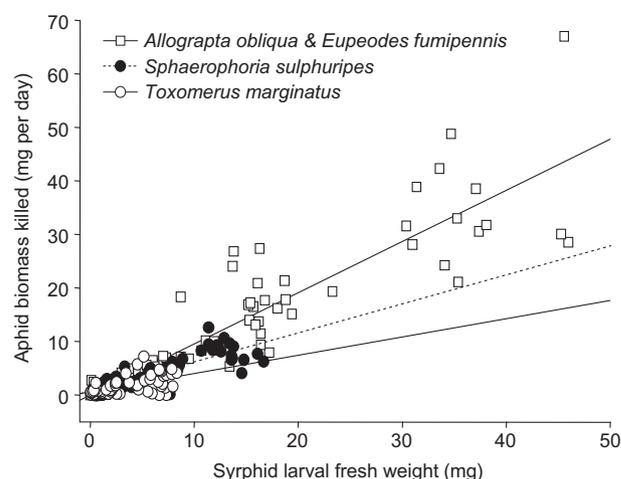

Fig. 4. Daily aphid biomass killed by larvae of four syrphid species in relation to fresh weight at 19.33 °C (±0.62 SD) and a 16:8 h L:D photoperiod. Linear relationships of the form $y = a + bx$ were fitted for each significantly different set of species; *Allograpta obliqua* and *Eupeodes fumipennis*, *Sphaerophoria sulphuripes* and *Toxomerus marginatus*. Fitted lines are significantly different among syrphid species ($P < 0.05$).
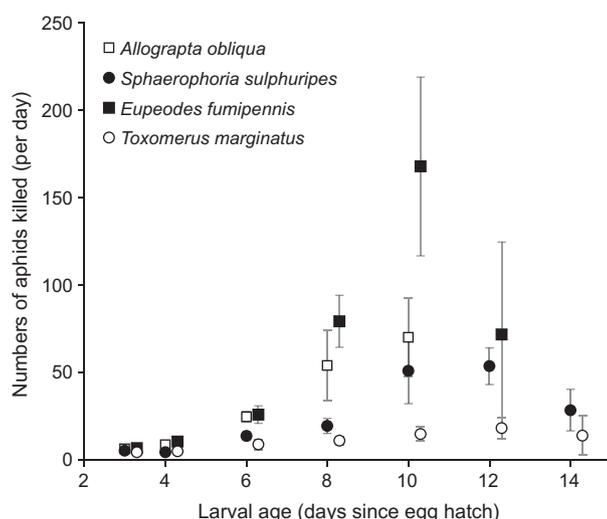
nis ($F = 0.63$ df = 2,225, $P = 0.53$), that *T. marginatus* had a lower daily aphid biomass-kill in relation to size than both *S. sulphuripes* and the aggregated *A. obliqua* and *E. fumipennis* ($F = 4.83$, df = 2,227, $P = 0.01$); and that *S. sulphuripes* had a lower daily biomass-kill in relation to size than the aggregated *A. obliqua* and *E. fumipennis* ($F = 18.61$, df = 2,227, $P < 0.001$).

For monitoring and non-monitoring days combined, the lifetime aphid biomass-kill for each species was estimated to be 87.91 mg (±20.42 SD) for *E. fumipennis*, 38.52 mg (±9.77 SD) for *A. obliqua*, 30.92 mg (±3.50 SD) for *S. sulphuripes*, and 19.53 mg (±04.93 SD) for *T. marginatus*. There was significant variation among species in the lifetime biomass-kill (ANOVA: $F = 71.81$, df = 3,47, $P < 0.001$); that for *E. fumipennis* was greater than for the other three species ($P < 0.001$), and that for *T. marginatus* was lower than for both *E. fumipennis* and *A. obliqua* ($P < 0.006$).

During larval development the mean cumulative aphid biomass killed on monitoring days was significantly greater than the mean cumulative aphid biomass consumed on monitoring days (Fig. 5) for *A. obliqua* ($W = 0$, $n = 17$, $P < 0.001$), *E. fumipennis*, ($W = 0$, $n = 15$, $P < 0.001$) *S. sulphuripes* ($W = 0$, $n = 11$, $P = 0.004$), and *T. marginatus* ($W = 0$, $n = 8$, $P = 0.007$).

Fig. 3. Mean (±95% CI) third-instar aphids killed daily in relation to larval age for *Allograpta obliqua*, *Eupeodes fumipennis*, *Sphaerophoria sulphuripes* and *Toxomerus marginatus* at 19.33 °C (±0.62 SD) and a 16:8 h L:D photoperiod.

4. Discussion

This study compared four syrphid species commonly found in California's lettuce fields in order to assess their potential for lettuce aphid suppression. When fed on lettuce aphid the development time of the syrphid species differed, with *A. obliqua* being the shortest and *T. marginatus* the longest. As *E. fumipennis* is the largest of the four species, followed by *A. obliqua*, *S. sulphuripes* and *T. marginatus*, larval development time does not appear to be related to body size. Our estimates of the development times of *A. obliqua* (21.8 days) were similar to those found for the same syrphid on an alternative aphid species (Jones, 1922). At a comparable temperature (20 °C), Diaz and Fereres (2005) report that the lettuce aphid required only 8–9 days for nymphal development, suggesting that the aphid can proceed through many generations during each syrphid generation. Moreover, as more aphids were consumed by the larger, older syrphid larvae this suggests that adult syrphids must oviposit on lettuce early in the crop cycle

sulphuripes and *T. marginatus* differed significantly only at ages 8, 10 and 12. For both monitoring and non-monitoring days combined the lifetime number of third instar aphids killed for each species was 507.19 (±175.32 SD) for *E. fumipennis*, 227.7 (±70.12 SD) for *A. obliqua*, 194.44 (±35.10 SD) for *S. sulphuripes*, and 131.61 (±21.62 SD) for *T. marginatus*. There was significant variation in the lifetime number of aphids killed among syrphid species (ANOVA: $F = 34.62$, df = 3,47, $P < 0.001$) with that for *E. fumipennis* being significantly greater than for the other three species ($P < 0.001$).

Analysis of the daily aphid kill as measured by biomass showed a significant interaction between larval fresh weight and species ($F = 1263.7$, df = 3,225, $P < 0.001$), indicating that larval fresh weight alone did not account for the aphid biomass-kill by the different species. To determine which species differed significantly in their daily capacity for aphid biomass-kill in relation to larval size, we compared species through stepwise a posteriori aggregation (Fig. 4). This showed that *A. obliqua* did not differ from *E. fumipen-*
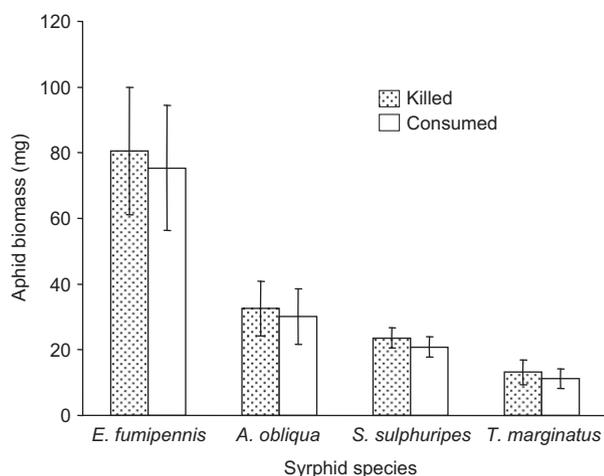
Fig. 5. Mean (±SD) cumulative biomass of aphids killed and consumed from monitoring days during the larval development of *Allograpta obliqua*, *Eupeodes fumipennis*, *Sphaerophoria sulphuripes* and *Toxomerus marginatus* at 19.33 °C (±0.62 SD) and a 16:8 h L:D photoperiod. The biomass of aphids killed is significantly different than that consumed for all four species ($P < 0.05$).

and establishment of aphid populations in order to be effective biological control agents.

Our study demonstrates that *E. fumipennis* killed the greatest number and biomass of lettuce aphids throughout its larval period, while the biomass of aphids killed by *T. marginatus* was the least. However, when larval fresh weight was taken into account, both *A. obliqua* and *E. fumipennis* had the same daily rate of aphid biomass killed in relation to size and a higher rate than each of the other two species. It is also interesting to note that the daily biomass killed by all four syrphid species peaked in the third instar at least one day prior to pupation (Fig. 3). This pattern was also found for *Episyrphus balteatus* (De Geer) in a similar study (Tinkeu and Hance, 1998) and suggests that the larvae feed less as they approach the prepupal stage in preparation for metamorphosis.

A number of studies have estimated the consumption rates of syrphid larvae and in most cases these are reported as per capita number of aphids killed for the complete larval period. While consumption rates can be greatly influenced by temperature (Tenhumberg and Poehling, 1995) and the suitability of different aphid species as prey (Short and Bergh, 2004), comparison of our results with those from previous studies show many similarities. For larger syrphids, comparable in size to *E. fumipennis*, estimates of lifetime aphids killed have varied from 298 first instar *Aphis fabae* for *Eupeodes confrater* (Wiedemann) (Sood et al., 2007), to 660–1140 third instar *Metopolophium dirhodum* (Walker) for *Episyrphus balteatus* (Tenhumberg and Poehling, 1995), with *Eupeodes corollae* (Fabricius) killing 867 medium-sized aphids (*Aphis fabae* and *Myzus persicae* (Sulzer) (Schneider, 1969), and *Scaeva albomaculata* (Macquart) killing 670 mixed instar *Brachycaudus amygdalinus* (Schouteden) (Nourbakhsh et al., 2008). Thus our estimate of 507 third instar *N. ribisnigri* killed over the lifetime of *E. fumipennis* is well within this range. Similarly, older larvae of *Sphaerophoria scripta* (Linnaeus) killed about 60 *Megoura viciae* Buckton daily (Schneider, 1969) compared to our estimate of a maximum of 54 third instar *N. ribisnigri* killed daily by *S. sulphuripes*. *Heringia calcarata* (Loew), a smaller syrphid species, was found to kill 105 first and second instar *Eriosoma lanigerum* (Hausmann) in its lifetime (Short and Bergh, 2004), compared to our estimate of 132 third instar *N. ribisnigri* killed in a lifetime by *T. marginatus*.

The maximum daily aphids killed by the syrphid larvae in our study varied from 168 for *E. fumipennis* to 18 for *T. marginatus*. These rates are higher than for many other groups of aphidopha-

gous predators. For example, comparable estimates of daily aphids killed by juveniles are 1–3 for spiders (Gavish-Regev et al., 2009), 3 for *Aphidoletes aphidimyza* (Rondani) and 4 for *Leucopis* spp. (Latham and Mills, 2010), 10 for *Macrolophus pygmaeus* Rambur (Fantinou et al., 2009) and 16 for *Anthocoris nemorum* (L.) (Simonsen et al., 2009), 14 for *Coccinella septempunctata* Linnaeus (Shannag and Obeidat, 2006) and 44 for (Atlhan et al., 2010), 35 for *Chrysoperla carnea* (Stephens) and 44 for *Chrysopa nigricornis* Burmeister (Latham and Mills, 2010). Thus, in comparing the syrphid species from our study to the other aphidophagous predator groups above, we concur with the previous literature that syrphids are one of the most important groups of aphid predators (Brewer and Elliott, 2004; Freier et al., 2007; Haenke et al., 2009; Tenhumberg and Poehling, 1995; Winder et al., 1994).

In contrast to our expectation, a significant interaction between larval fresh weight and syrphid species indicated that body size alone does not account for the daily aphid biomass killed. Thus there appear to be species-specific differences in predation capacity relative to body size for syrphids feeding on the same aphid species. These results have important implications, as it cannot be assumed that syrphid species can be grouped by body size alone to extrapolate laboratory-based estimates of predation potential to the field. We also demonstrated a significant difference between biomass killed and consumed for the four syrphid species in this study, similar to that found for larvae of the chrysopid *Chrysopa nigricornis* (Latham and Mills, 2009). Although currently unexplored (Cohen, 1995), this suggests that syrphid larvae may either utilize extra-oral digestion or that their mouthparts do not allow full extraction of the biomass available in each prey item.

It is clear from our results, that the two larger syrphid species, *E. fumipennis* and *A. obliqua*, have a greater capacity for control of the lettuce aphid, *N. ribisnigri*, than the two smaller species *S. sulphuripes* and *T. marginatus*. Thus the intercropping of lettuce with flowering plants to provide floral subsidies that attract adult syrphids could benefit from a greater focus on these larger species. It has been found that adults of some syrphid species are highly selective in their pollen diets while others are generalists. The mechanisms for syrphid specialization on floral resources are still unclear, but flower color seems to play a partial role (Haslett, 1989). In addition, from observations in Oregon, cilantro appeared to be more frequently visited by smaller to medium sized syrphids such as *Allograpta micrura* (Osten Sacken), *S. sulphuripes* and *Toxomerus* spp., while phacelia was visited more frequently by large syrphids such as *Eupeodes lapponicus* (Zetterstedt), *Meliscaeva cinctella* (Zetterstedt), *Scaeva pyrastri* (L.), and *Syrphus opinator* Osten Sacken (Colley and Luna, 2000). Another study from Oregon found that in one location, *E. fumipennis* visited phacelia more frequently than alyssum whereas no preference occurred in another location (Ambrosino et al., 2006). Thus, these apparent preferences may be influenced by interactions with other pollinators (Ambrosino et al., 2006; Hogg et al., 2011) and by temporal and spatial changes in the floral resources available in the surrounding environment (Smith and Chaney, 2007). The data obtained from this study on the daily feeding capacity of four common syrphid species associated with lettuce aphid in central coast lettuce fields provides a valuable first step in understanding the predation potential of syrphids in the biological control of this invasive pest.

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