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Life table and predation rates of the syrphid fly *Allograpta exotica,* a control agent of the cowpea aphid *Aphis craccivora*

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Abstract

Larvae of *Allograpta exotica* (Wiedemann, 1830) (Diptera: Syrphidae) are important natural enemies of common agricultural pests such as aphids (Hemiptera: Aphididae). Life history, life table and functional response of *A. exotica* were determined using the cowpea aphid *Aphis craccivora* Koch, 1854 as prey under controlled conditions of temperature, humidity and light. The average recorded duration of *A. exotica* development was 2.0, 7.4 and 5.7 days for eggs, larvae and pupae respectively, and 15.04 days from egg to adult emergence. The adult longevity was not significantly sex dependent, but imagoes lived longer than in previous studies. The offspring sex ratio was favorable to males. The mortality and survival rate were recorded on a daily basis for all immature stages and adults. The age specific survival rate was determined and the highest mortality occurred in eggs followed by mortality in 1st and 2nd instar larva. Moreover, in the present study different levels of aphid densities 10, 30, 40, 50, 60, 70, 80 and 100 were used to calculate the functional response. Based on logistic regression analyses the three instar larvae and the whole larval stage (first to third instar) exhibited a type II functional response. Handling time was shortest for the third larval instar followed by second and first instars. Potential use of *A. exotica* in augmentative biological control is discussed.

Key words

Diptera, Syrphidae, Aphididae, biological control, functional response

1. Introduction

The genus *Allograpta* Osten Sacken, 1875 (Diptera: Syrphidae) is world-wide distributed except in the Polar regions and most of the Palearctic Region (Vockeroth, 1969; Mengual et al., 2009). Adults are flower visitors and are important pollinators in natural ecosystems and agricultural crops (Vockeroth and Thompson, 1987; Ssymank and Kearns, 2009; Rotheray and Gilbert, 2011). The larvae of most *Allograpta* species are predators of hemipteran pests (see Rojo et al., 2003 for a review of published prey records) and represent effective biological control agents (BCA) (Bugg et al., 2008; Smith et al., 2008). The larvae have such voracity that enables them to reduce aphid populations and to exercise control over these insect pests (Schneider, 1969; Nelson et al., 2012).

The species *Allograpta exotica* (Wiedemann, 1830) is widespread in the New World, ranging from United States south to Argentina and it has been introduced in Hawaii (Hardy, 1964; Thompson, 2013). *A. exotica* is abundant in its natural range and a common aphidophagous species in several crops of economic importance (Rojo et al., 2003; Bugg et al., 2008). Adult preferences of *A. exotica* have been studied in relation to their phenology (Greco, 1995), diurnal activity (Salto et al., 1994) or in order to recommend the use of specific flower plant species in flower strips composition to increase the presence of this flower fly (Salto et al., 1991). Furthermore, identification keys for immature stages and adults are found in the literature (Greco, 1998; Castro and Araya, 2012; López et al., 2012) and facilitate species recognition in the field and in the laboratory.

Although *A. exotica* has been documented feeding on many aphid pests (Silva et al., 1968; Cermeli, 1983 for records in Venezuela; Rojo et al., 2003 and references therein; López et al., 2003; Resende et al., 2006; Smith and Chaney, 2007; Manfrino et al., 2011; Sturza et al., 2011), studies about its biology are rare. Cevallos (1973) presented data about the collection, rearing, preparation/mounting and morphology of *A. exotica* using *Rophalosiphum maidis* (Fitch, 1856) as prey. Salto et al. (1994) studied the ingestion capacity of *A. exotica* over the aphid *Schizaphis graminum* (Rondani, 1852) in laboratory conditions. Greco (1998) gave some details about parasitoids, predators and entomopathogenic fungus attacking *A. exotica*. More recently, Castro and Araya (2012) described the general biology for the genus *Allograpta* by comparing the life cycle of several species of this genus, including *A. exotica*.

Aphis craccivora Koch, 1854, commonly known as cowpea aphid or black legume aphid, is distributed worldwide, but particularly common in warm temperate and tropical regions. It is a very important polyphagous pest, feeding on over 80 plant families with preference for the family Fabaceae (Blackman and Eastop, 2000). It is considered an economically important pest on legumes as *Arachis hypogaea* L. (peanut), *Cajanus cajan* (L.) Millsp. (pigeon pea), *Canavalia ensiformis* (L.) DC (jack-bean), *Phaseolus vulgaris* L. (common bean), and *Vigna unguiculata* (L.) Walp. (cowpea) among others (Cermeli, 1970). Furthermore, *A. craccivora* is vector of about 30 plant virus diseases; including the Tobacco etch virus (TEV) (Herold, 1970, 1972) and the Papaya ring spot virus (PRSV) (Vegas et al., 1986, 2004), which may destroy the plantations of these crops.

Up to 44 different species of predatory flower flies, from 15 distinct genera, have been reported feeding on *A. craccivora*, including two species of the genus *Allograpta*, i.e. *Allograpta javana*

(Wiedemann 1824) and *Allograpta obliqua* (Say 1823), but not *A. exotica* (Rojo et al., 2003). Most of these records are from the Palaearctic, Oriental (mostly India and Pakistan), and Afrotropical Regions, but there are records also from Australia and U.S.A. *Toxomerus dispar* (Fabricius, 1794) is the single syrphid species recorded in the Neotropical Region feeding on this pest species from Brazil.

In order to evaluate *A. exotica* as BCA of aphids some population characteristics need to be determined, such as growth and predation rates. The key components for this type of evaluation are predation rate assessments and life table studies, because they can provide a comprehensive description of the species' development and survival. The rate at which predators attack prey is to some extent dependent on prey density. This relationship has been defined as the functional response (Solomon, 1949) and it is one of the most important factors in the population dynamics of predator-prey systems (Schenk and Bacher, 2002). The functional response concept was first described by Holling (1959) and has been widely used to evaluate and predict the potential effectiveness of predators as BCAs (Laing and Osborn, 1974; Everson, 1980; Sabelis, 1985; Trexler et al., 1988; De Clercq et al., 2000; Badii et al., 2004; Reis et al., 2003, 2007; Sepúlveda and Carrillo, 2008; Timms et al., 2008; Hassanpour et al. 2009).

Despite the potential of *A. exotica* for aphids' control, no information is available about its predator-prey interactions. This information is essential to predict the efficiency of *A. exotica* as a biological control agent of aphids. Thus, the main objective of this survey was to study under laboratory conditions the performance of larvae of *A. exotica* feeding on *A. craccivora*. Consequently, in order to evaluate the potential of *A. exotica* as BCA of the economically important pest *A. craccivora*, two main objectives were defined for the present study: (i) to estimate the age-state, two-sex life table of *A. exotica* fed with *A. craccivora*; and (ii) to determine the type of functional response and to estimate the parameters of attack rate (*a*) and handling time (T_h) of the three larval instars of *A. exotica*.

2. Material and methods

2.1. Aphid and syrphid cultures

The aphid colony of *A. craccivora* used for this study was obtained from a laboratory culture, which has been maintained as clones at the Entomology laboratory at the Universidad Centroccidental Lisandro Alvarado (UCLA) for some years. *A. craccivora* were reared on cowpea leaves (*Vigna unguiculata* (L.) Walp. var. Tuy) in a rearing chamber at 25 ± 2 ºC and 68 ± 10% RH, with a constant photo-regime of 12L:12D following the methodology of Arcaya (2000). Cowpea plants were sown in a polythene plastic pot (350 cm^3) containing black soil and earthworm compost as substrate. Using a camel's hair brush, 6–8 gravid aphids were placed on individual cowpea plants with at least two true leaves. Aphid culture was maintained by the addition of suitable seedlings three times a week. Extra plants were also grown to provide additional leaves for the Petri dish experiments.

Adults of *A. exotica* were collected using a standard hand net of 30.5 cm of diameter at 1,633 m.a.s.l. in horticultural crops at Finca Las Lajitas, sector Monte Carmelo, in the municipality of Andrés Eloy Blanco (Lara State, Venezuela). Field collected males and females were introduced into glass vials (21 mm x 70 mm). Inside each vial, honey was applied in rows to feed the adults. The vial was covered with a thin mesh held by a rubber band, which allowed a proper relative humidity and air circulation. Once the field collecting was over, samples were taken to the Entomology laboratory at UCLA, in Tarabana, situated circa 100 km from the sampling point.

In the laboratory, adult females of *A. exotica* were transferred into a plastic rearing cage (50 cm x 38 cm x 35 cm) covered with a thin mesh. To obtain a proper relative humidity and air circulation, rectangular openings were made in the walls of the plastic cage, which were later covered with mesh. Two opened Petri dishes of 10 cm of diameter were used to supply the food. Internal surface of the Petri dish was covered with absorbent paper, and small glass jars were placed in each plate at inverted position; one jar containing a honey solution at 50% and the other jar with distilled water. In addition, a glass tub (21 mm x 70 mm), with a bouquet of flowers of the plant *Tridax procumbens* L., was located in the cage to supply pollen as a protein source for the fly individuals. A 15 days old cowpea plant (*V. unguiculata*), infested with the aphid *A. craccivora*, was also placed in each cage to stimulate the oviposition (Schneider, 1969). Plants were checked every four hours and leaves with syrphid eggs were taken and isolated. Flower flies were maintained in a rearing chamber at 25 ± 2 ºC and 68 ± 10% RH with a constant photo-regime of 12L:12D.

2.2. Life table study and analysis

For the life table study, a total of 100 eggs of *A. exotica* were transferred into Petri dishes of 10 cm of diameter (1 egg per plate) with an opening in the lid covered with thin mesh. Each plate was labelled accordingly with the oviposition date and covered with absorbent paper, and a cowpea leaf with aphids was also provided as prey. After the predatory larvae hatched, each larva was daily fed with more than 100 *A. craccivora* of mixed ages. At the end of the larval development, the obtained pupae were transferred and placed individually into another Petri plates. The emerged adults were placed in cages such as the ones already explained above for the wild-collected adults. They were daily fed with fresh pollen of *T. procumbens*, water and honey as detailed previously. All developmental stages were evaluated daily at the same time in order to record the number of days that each individual spent in each stage.

Raw data on the survivorship and longevity were analyzed according to the age-stage, two-sex life table (Chi and Liu, 1985; Chi, 1988). The age-stage specific survival rate (*Sxj*), where *x* is the age and *j* the stage, the age-specific survival rate (*lx*) and the age-stage specific life expectancy (*exj*) were calculated accordingly. The life expectancy indicates the life span that an individual of age *x* and stage *j* is expected to live. Note that this methodology considers each instar (i.e. first, second and third instar larva) as different "stages" of the syrphid life cycle in the same way that egg, pupa and adult. The computer program TWOSEX-MSChart (Chi, 2014), designed in Visual basic for the Windows operating system, was used to facilitate raw data analysis. This program is available at http://140.120.197.173/Ecology/ (Chung Hsing University) and at http://nhsbig.inhs.uiuc.edu/wes/chi.html (Illinois Natural History Survey).

2.3. Functional response experiments

The experimental arena consisted of Petri dishes of 9 cm of diameter prepared as in the previous experiment. To determine the impact of prey densities on larval performance of *A. exotica*, eight treatments corresponding to eight prey densities were conducted, in which 10, 30, 40, 50, 60, 70, 80 and 100 individuals of third and fourth instar nymphs of *A. craccivora* were provided to a single syrphid larva on a cowpea leaf inside the Petri dishes. Larvae were observed every 12 hours. The number of aphids consumed was recorded each 24 hours and then, each syrphid larva was transferred to a new Petri dish and supplied with new aphids. The number of replicates was 8 for each treatment.

Third and fourth instar nymphs of *A. craccivora* are enough to supply the nutrition requirements of the syrphid larvae, and the prey density using them is much lower than when first and second instar nymphs are used, making the preparation of the experiment and the evaluation of the results less time-consuming. Adults of *A. craccivora* are avoided in the functional response experiments to avoid the potential new offspring from gravid females, which would underestimate the consumption of prey.

2.4. Functional response analysis

In predator-prey interactions, the functional response of predators describes the per-capita predation rate, and a variety of models have been developed: Holling type II and III (Holling, 1959); Beddington (1975); Arditi and Ginzburg (1989); Arditi and Akçakaya (1990); and θ-sigmoid (Turchin, 2003) (Table 1). According to Okuyama and Ruyle (2011) all these existing functional response models can be described in general form by the following equation:

$$dN \div dt = -\lambda P \div (Q + \lambda h)$$

where N and P are the density of the prey and the predator, respectively; h is the handling time and $\lambda = aN^z$ is related to the capture rate, with a and z being positive parameters. The term Q is either a constant or a function of P (Table 1). When $Q = 1$, then $\lambda = aN$ corresponds to the

Holling type II model, and $\lambda = aN^2$ corresponds to the Holling type III model. If z is now regarded as a non-predetermined parameter in $\lambda = aN^z$, so that a, h and z are allowed to vary in finding the best fit, then equation is the θ-sigmoid model (Turchin, 2003). In the present study, since the number of predators is always 1, the Arditi and Ginzburg and Arditi and Akçakaya models have not been applied because the results are the same as Holling type II model (Table 1).

Four functional response models (Holling type II and III, Beddington-DeAngelis, and θ-sigmoid) were used to estimate the parameters of attack rate (a) and handling time (h). These parameters were estimated with R function *fr.ssq* proposed by Okuyama and Ruyle (2011). This function uses the *optim* function to minimize the sum of squares.

According to Okuyama (2013) the best model was selected using a general model selection method, concretely the Akaike information criterion (AIC):

$AIC = \log (SSQ_k) + 2*k/n$

(Hilborn and Mangel, 1997) where SSQ_k is the minimum sum of squares for the model with k parameters and n is the number of observations.

2.5. Statistical methodology

Data obtained from the studies of life cycle, number of consumed prey, and longevity were analyzed using descriptive statistics (mean and standard error). A one-way analysis of variance (ANOVA) was performed to compare differences in the number of prey killed by the three larval instars and the total larval stage of *A. exotica* among various prey densities. When the overall

ANOVA was significant, differences among treatment categories were determined using the Bonferroni test ($P<0.05$) (SPSS, 2008).

3. Results

3.1. Life table study

The life cycle of *A. exotica* from egg to the adult emergence was 15.04 ± 0.13 days long (mean ± standard error), with a variation range between 12 and 16 days (Table 2, Figure 1). Eggs hatched after two days from oviposition. Larvae had an average developmental time of 7.4 ± 0.14 days, with a variation range between 5 and 8 days. First larval stadium (L1) and second stadium (L2) had duration of two days each, but the third larval stadium (L3) took three to four days. Lastly, the pupae had an average developmental time of 5.7 ± 0.08 days, varying between 5 and 6 days.

Out of the cohort of 100 eggs collected at the beginning of the life table study, 66 eggs hatched successfully, and out of these 50 emerged as adults. At the end, 31 males and 19 females were obtained, with a sex ratio of 1:0.61 showing prevalence of males. The longevity data were very similar between males and females (see Table 2), without significant differences between sexes ($P>0.05$).

The age-stage specific survival rate (S_{xj}) denotes the probability that a newly laid egg will survive to age x and stage j. These curves also show the survivorship and stage differentiation (Figure 2). For example, the probability that a new-born egg survives to the larva stage is 0.66, to the pupal stage is 0.52 and to adult stage is 0.31 for males and 0.19 for females. The l_x is the probability that a newly laid egg will survive to the age *x*, thus, the curve *lx* is a simplified version of *Sxj* (Figure 2). The highest mortality rate was 0.34 and occurs during the egg stage. Mortality rates observed during the larval stage decreased as larval development progressed, from 0.14 for the first instar larva to 0.09 and 0.02 for the second and third instar larva respectively. During the pupal stage the mortality was hardly reduced to 0.04.

The overlaps between different stages during developmental period demonstrate the variable developmental rates among individuals (Figure 2). Consequently, individuals of the same age but different stage/instar may have different life expectancies. The age-stage-specific life expectancy (*exj*) (Figure 3) is the lifespan remaining for an individual of age *x* and stage *j*. For example the life expectancy of a new egg is 15 days, but this parameter increase to 20 days for the first instar larvae due to the high mortality of the eggs, afterwards the life expectancy decreasing progressively with age (Figure 3). The pattern of life expectancy for males and females was very similar (Figure 3).

3.2. Prey consumption of *Allograpta exotica* larvae fed on different prey densities

Mean number of aphids consumed per day by *A. exotica* during total larval stage increased significantly with prey density, reaching the maximum value when 80 preys were provided (i.e. 23.34 ± 0.81 aphids/day) (F = 8.09, p< 0.0001), although there is no statistical significant difference with densities higher than 50 aphids (Table 23). Only in the case of the third instar, the voracity of the larva increased significantly with prey density (L3: F = 37.84, p< 0.0001), reaching the maximum value of consumed prey also at a density of 80 aphids. On the other hand, first and second instars satiation was attained at a lower prey density, that is, when 10 and 30 preys were provided (i.e., 4.50 ± 0.63 and 10.25 ± 0.51 aphids/day were consumed, respectively). With higher prey densities, first and second instars did not have a statistical significant difference among density treatments.

Larvae of *A. exotica* showed different voraciousness in relation to their development in all of the densities tested. For example, for the density of 30 aphids the mean number of aphids eaten was 4.81, 10.25 and 26.54 aphids/day during first, second and third larvae stadium respectively (Table 3). In all studied densities the mean number of aphids consumed per day by the second instar larvae was more than the double of the aphids eaten by the first instar and the consumption of the third instar was three times the consumption of the second instar (1:2:3 ratio among instars). The total number of consumed prey (from first to third larval instar) also increased with higher prey density, from 109.7 aphids at a density of 30 aphids/day to 163.4 aphids at a prey density of 80 aphids/day (Table 4).

3.3. Functional response

The functional response of the three larval instars and the total larval stage (L1+L2+L3) of *A. exotica* to third and fourth instar nymphs of *A. craccivora* are depicted in Figure 4. For the first instar the fit is not good for any of the models studied, since the density of prey offered to the larvae was too high (Fig. 4a). In the case of the second larval instar, the Holling type II and the θ-Sigmoid models produced almost identical fits to our data (Fig. 4b; Table 5). Third instar larvae, however, showed a similar fit to Holling type III and Holling type II functional response to the prey (Fig. 4c; Table 5). Finally, the total larval stage presented a Holling type II functional response (Fig. 4d; Table 5).

The estimated values for attack rates and handling times of the three larval instars are shown in Table 5. According to Holling type II model, the attack rate was found to be highest for the third larval instar (a = 0.249) followed by the first instar (a = 0.089), the second instar (a = 0.059) and for the whole larval stage (a = 0.074). Handling time (h) was 0.87 for the whole larval stage, being the shortest for the third larval instar (h = 0.54) followed by second and first instar (h = 1.5 and h = 4.5, respectively). These parameters for the third instar larvae following a Holling Type III model were a = 0.024 and h= 0.597.

4. Discussion

4.1. Life table study

Our results for the life cycle of *A. exotica* showed a relatively small standard error for the preimaginal stages (egg, larva and pupa), but higher deviation in the adults. The life cycle of *A. exotica* from egg to the adult emergence was 15.04 ± 0.13 days long, which is shorter than the estimated life cycle for the same species in previous studies. Cevallos (1973) reported a variation range in the life cycle of *A. exotica*, fed with *R. maidis*, of 19.5 to 21.5 days long. More recently, Oliveira and Santos (2005) obtained an average duration of 20.2 days for the life cycle of this syrphid fed with eggs and nymphs of the whitefly *Bemisia tabaci* (Gennadius, 1889) biotype B. However this predator-prey relationship is doubtful. Oliveira et al. (2003) reported *A. exotica*, so far a species exclusively aphidophagous, feeding on two important whitefly species pests, *B. tabaci* biotype B and *Trialeurodes vaporariorum* Westwood, 1856 (Hemiptera: Aleyrodidae). Specimens identified as *A. exotica* in Oliveira et al. (2003) and in Oliveira and Santos (2005) may belong to the morphologically closely related species *Allograpta obliqua* (Say, 1823), which has been reported feeding on three different taxa of whiteflies, including *B. tabaci* from Mexico (Resendiz-Ruiz, 1993). *A. obliqua* is also a well-known aphidophagous flower fly with potential as BCA (Smith and Chaney, 2007; Noma and Brewer, 2008; Hopper et al., 2011) but immature stages of both *Allograpta* species are not yet distinguishable using morphology (Arcaya, 2012).

A more detailed analysis of the life cycle shows that the main difference among studies is the length of the larval stage. In both former works (Cevallos, 1973; Oliveira and Santos, 2005) the larval period is nearly twice longer than the larval period in the present study. As in other predatory species our results suggest that the length of the life cycle of *A. exotica* is dependent of the prey and most probably of the number of prey individuals (Hemptinne et al., 1993; Almohamad et al., 2009). As indicated by Omkar and Srivastava (2003), there might be more optimal prey species in terms of nutrients and proteins source rather than *A. craccivora* for the mass rearing of *A. exotica*, but the best results in terms of larval period length have been obtained with *A. craccivora* so far and this prey is an excellent initial candidate for this purpose.

Oliveira and Santos (2005) studied the adult longevity of *A. exotica* using three different diets: 1) honey and yeast; 2) honey, yeast and pollen; and 3) sugar, yeast, and pollen. Using these diets, they obtained an average adult longevity of 5.3, 6.0 and 13.2 days respectively. The second diet is the closest one to the diet used in our study, i.e. fresh pollen of *T. procumbens* and diluted honey in water. However, imagoes in the present study lived almost two times longer (12.97 ± 1.98 days for males, and 11.58 ± 2.44 days for females). We think that this important difference is due to the use of fresh pollen in our research, although syrphid species surveyed in both studies might be different as indicated above.

The sex ratio of the offspring was favorable to males. This result is in concordance with the study by Belliure and Michaud (2001) using a different syrphid species, *Pseudodoros clavatus* (Fabricius, 1794), where the sex ratio was 2:0.97 (male:female). Per contra, Torrealba (2009) reported a sex ratio of 1:1 for the same species, *P. clavatus*.

For most insects, the developmental rates vary among individuals and between the sexes (Istock, 1981; Chi and Liu, 1985; Carey, 1993). Chi and Liu (1985) and Chi (1988) noted that neglecting the variable developmental rate and the male population might cause errors in calculating the age-specific survival rate. These authors developed an age-stage, two-sex life table that takes stage differentiation and the male population into consideration (Chi and Liu, 1985; Chi, 1988), and their methodology has been used to describe the population characteristics of many insect and mite species under the influence of a variety of physical conditions (Grabe et al., 2005; Huang and Chi, 2012; Yu et al., 2013).

Our results for the age-stage specific survival rate (*Sxj*) of *A. exotica* showed significant overlapping between stages curves (Figure 2) due to the variable developmental rate among individuals of each stage, i.e. egg, first instar, second instar, third instar and pupa. Traditionally only female age-specific survival rate (*lx*) was calculated and those overlapping curves were not observed. Comprehensive discussion on the problem of female age-specific life tables can be found in Chi (1988), Yu et al. (2005), Chi and Su (2006), and Huang and Chi (2012). On the other hand, life expectancy (*exj*) of *A. exotica* decreased gradually with aging with a maximum of 20.98 days (Figure 3). One major reason is that our study was conducted under laboratory conditions, without the adverse effects of field conditions and exposure to natural enemies or parasitoids.

4.2. Functional response

Effects of prey density frequently vary with developmental stage since voracity increases with larval development (Barlow and Whittingham, 1986; Omkar and James, 2004; Putra and Yasuda, 2006; Mushtaq et al., 2014). In the present study, all larval instars of *A. exotica* had a high predation on third and fourth instar nymphs of *A. craccivora*, with the third instar larva being the most voracious. At high densities of *A. craccivora* nymphs, the mean number of prey consumed by the third larval instar of *A. exotica* was 40.9 aphids, indicating its potential for pest control. The higher predation of the last instar is a logical reflection of the larger size, as well as its extra requirement of nutrients during their subsequent non-feeding pupal stage.

There are only a few papers about functional response of predatory syrphids, being most of them focus on the cosmopolitan species *Episyrphus balteatus* (De Geer, 1776) (e.g. Tenhumberg, 1995; Putra and Yasuda, 2006; Jalilian et al., 2011; Sobhani et al., 2013; Amiri-Jami and Sadegui-Namaghi, 2014). In the Neotropical Region where *E. balteatus* is absent, only the functional response of *Pseudodoros clavatus* (Fabricius, 1794) has been studied (Torrealba and Arcaya, 2014). Although functional response of Holling types I, II and III have been reported for syrphids, the functional response type II is the most common. For instance, functional response type II has been reported for *E. balteatus* and *Scaeva albomaculata* (Macquart, 1842) feeding on *Myzus persicae* (Sulzer, 1776) (Jalilian et al., 2011), for *E. balteatus* upon *Aphis fabae* Scopoli, 1763 (Amiri-Jami and Sadegui-Namaghi, 2014), and for *P. clavatus* upon *A. craccivora*

(Torrealba and Arcaya, 2014). Type II functional response is also detected by Khan et al. (2016) for *Sphaerophoria scripta* (Linnaeus, 1758) and *E. balteatus* upon *Aphis pomi* (de Geer, 1773). Khan et al. (2016) also reported a type II functional response for two non-predatory flower flies, i.e. *Eristalis tenax* (Linnaeus, 1758) and *Eristalis interruptus* (Poda, 1761); clearly a misidentification or a mistake. However, other studies report different results. This is the case Tenhumberg (1995) found a type III functional response for *E. balteatus* feeding on *Sitobion avenae* (Fabricius, 1794) and *Metopolophium dirhodum* (Walker, 1849), and Sobhani et al. (2013) reported a type III functional response of the third instar of *E. balteatus* on *Aphis gossypii* Glover, 1877. On the other hand, Chitra Devi and Singh (2000) found a type I functional response for *Ischiodon scutellari*s (Fabricius, 1805) preying on *Lipahis erysimi* (Kaltenbach, 1843).

Our results revealed that different larval stages of *A. exotica* exhibited different types of functional response to the offered prey. According to our findings *A. exotica* can show both Holling type II and Holling type III responses, supporting the perception of a single syrphid predator species being able to exhibit different responses depending on e.g. predator size and age and prey species and size (Singh and Mishra, 1988; Putra and Yasuda, 2006; Jalilian et al., 2011; Sobhani et al., 2013). More detailed studies considering different preys, precise statistical analyses and the effect in the different larval instars are required to know the specific details of the functional response of predatory syrphid larvae. The functional response of most polyphagous predators is one of the key aspects to consider their use as BCAs (Murdoch and Oaten, 1975), but field-based studies are always needed to confirm experimental results under controlled conditions (Pervez and Omkar, 2005; Montoya-Alvarez et al., 2010).

Another important variable of a potential BCA is the handling time (*h*). The estimated *h* based on functional response models differ from the actual handling time obtained by direct observations, because the parameter *h* encompasses the time spent not only on actual prey handling but also on other non-searching behavior such as resting and pruning (Holling, 1965; Hassell, 1978). Nevertheless, the comparison of *h* values obtained from different studies conducted and analyzed in a similar approach may be of relevance (Enkegaard et al. 2001). According to the Holling type II model the *h* obtained in the present study for the three larval instars of *A. exotica* feeding on *A. craccivora* nymphs (L1=4.5 h, L2=1.5 h, L3=0.54 h) is higher than the *h* obtained by Jalilian et al. (2011) for the larval instars of *E. baltuatus* and *S. albomaculata* feeding on *M. persicae* (*E. balteatus*: L1=2.26 h, L2=0.51 h, L3=0.32 h; *S. albomaculata:* L2=0.56 h, L3=0.25 h).

As mentioned before, life table studies and growth and predation rates are the crucial factors to evaluate the performance of a BCA. *A. exotica* fed with *A. craccivora* shows variation in the developmental rates, mostly on the third larval instar and pupal stages, but the longevity of adults is independent of the sex; although the sex ratio is definitively biased towards males. In addition, the prey consumption varies between developmental stages and prey densities, being the third instar larva the most voracious stage (showing the highest attack rate and the shortest handling time as well) and having a density optimum at 80 preys.

These results show the potential of *A. exotica* as a BCA of *A. craccivora*, a very promising BCA as one specimen of *A. exotica* can consume over 163 aphids (Table 4) and it develops faster than feeding on other prey species, i.e. it has a shorter life cycle. Salto et al. (1994) studied the ingestion capacity of *A. exotica* over the aphid *Schizaphis graminum* (Rondani, 1852) in laboratory conditions. Their results showed a direct relationship between pupa and adult size and the ingestion level and concluded that a single larva of this syrphid species can consume up to 165 aphids before pupation. Present results are in agreement with Salto et al. (1994).

Adults live enough to mature and lay eggs, and we like to highlight that the adult stage of *A. exotica* represents circa the half of the life cycle of this species. These data imply that adult colonies can be self-sustainable in time, providing offspring that could be commercialized. Mortality after first larval instar is attenuated, which may indicate this as a good developmental stage for commercialization of living specimens. For the first time, *A. exotica* is reported feeding on *A. craccivora* in laboratory conditions, a new prey record for the syrphid species. Moreover, it is significant to point out that the only known flower fly feeding on *A. craccivora* in the Neotropics is *Toxomerus dispar* (records from Brazil), a fact that gives more relevance to the present study as only *A. exotica* has been successfully reared in laboratory conditions to feed in this pest species in the whole Neotropical Region.

Syrphid species are well-known and widely studied in the biological control of invertebrate pests, and it has been proved they reduce the populations of the pest species (Freier et al., 2001; Schmidt et al., 2004; Nelson et al., 2012). Several researches have studied the potential use of this group of predators to control particular pest (Rojo and Marcos-García, 1997; Michaud, 1999, 2002; Bergh and Short, 2008). In this study, the knowledge about the life cycle of *A. exotica* and the predator-prey relationship with *A. craccivora* under laboratory conditions (type of functional response) has improved as the first step to investigate the suitability of *A. exotica* to become used in augmentative biological control. Cock et al. (2010) listed the most important BCAs used in augmentative biological control based on the number of countries that used them, and among the top 25 only one syrphid appeared, *Episyrphus balteatus*. *Episyrphus balteatus* is used mainly in

Europe to fight against aphid pests since 1990, and it is the only syrphid species commercially available worldwide (van Lenteren, 2012). Recently, other syrphid species had been proposed as effective BCAs, this is the case of *Sphaerophoria rueppellii* (Wiedemann, 1830) on Mediterranean greenhouse crops (Amorós-Jiménez et al., 2014). In this sense it is important to note that genera *Sphaerophoria* and *Allograpta* are phylogenetically very close related (Mengual et al., 2008).

More research is needed to develop a full protocol of mass rearing for *Allograpta* species, especially *A. exotica*. Our study showed the importance of fresh pollen to maintain adults of *A. exotica* longer in captivity and the possibility to use *A. craccivora* as prey in mass rearing. Accordingly, we strongly believe that this kind of research might result in more syrphid species used in conservation biological control (see Pineda and Marcos-García, 2008a, 2008b) as well as augmentative biological control (Amorós-Jiménez et al., 2014). Van Lenteren (2012) only reported *Aphidius ervi* (Haliday, 1834) (Hymenoptera: Braconidae) and *Chrysoperla carnea* (Stephens, 1836) (Neuroptera: Chrysopidae) as BCAs of aphids in Latin America used in augmentative biological control. We want to encourage and promote the biological studies of syrphids to use them as BCAs in Latin America. The current low variety of BCAs and the fact that different groups of natural enemies may have a dissimilar actions on the prey, or different prey stages as targets, make unlikely that the use of more than one BCA increases interspecific competition (Letourneau et al., 2009; Messelink et al., 2013), what at the end is beneficial for the environment and commercial activities.

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Table 1

Different functional response models (modified from Okuyama and Ruyle (2011)). N: number of preys; P: number of predators; a: attack rate; h: handling time; θ: is a parameter and a specific value is not assumed; m: interference coefficient (this parameter is 0 for pure prey-dependence and 1for pure ratio-dependence). The term Q is either a constant or a function of P.

Common names	**Model**	z	**Q**
Holling type II	$aN \div (1 + ahN)$	1	1
Holling type III	$aN^2 \div (1 + ahN^2)$	2	1
θ-sigmoid	$aN^\theta \div (1 + ahN^\theta)$	θ	1
Beddington-DeAngelis	$aN \div (1 + \gamma P + ahN)$	1	$1 + \gamma P$
Arditi and Akçakaya	$aNP^{-m} \div (1 + ahNP^{-m})$	1	P^{-m}
Arditi and Ginzburg	$aN \div P \div (1 + ahN \div P)$	1	P

Table 2

The developmental time of each stage (days) and adult longevity (days) of *A. exotica*. SE = Standard error.

Parameter	**Stage**	**Mean ± SE**	**n (observations)**
Developmental time (days)	Egg	2	66
	Larva (L1)	2	58
	Larva (L2)	2	53
	Larva (L3)	3.4±0.14	52
	Larva (L1-L3)	7.4±0.14	52
	Pupa	5.7±0.08	50
	Total preadult stages	15.04±0.13	50
Adult longevity (days)	Female	11.58±2.44	19
	Male	12.97±1.98	31

Table 3

Predation rates (aphids/predator) of *A. exotica* fed with *A. craccivora* at different densities. Values within the columns followed by the different letter were significantly different at 0.05% level. ** Life cycle not completed

Prey density	**1st instar (L1)**	**2nd instar(L2)**	**3rd instar (L3)**	**mean larval stage**
10	4.50 ± 0.63ab	9.0 ± 0.35a	9.45± 019a	**
30	4.81 ± 0.63ab	10.25 ± 0.51a	26.54 ± 0.59b	15.68 ± 0.33a
40	3.69 ± 0.41b	9.63 ± 1.35a	31.33 ± 1.72bc	17.23 ± 1.19ab
50	4.50 ± 0.54ab	13.00 ± 1.21a	35.71 ± 1.37cd	20.30 ± 0.38bc
60	4.31 ± 0.41ab	12.38 ± 1.42a	37.42 ± 2.10ce	20.80 ± 0.83bc
70	4.13 ± 0.39ab	13.13 ± 1.59a	40.5 ± 1.30de	21.39 ± 1.18c
80	6.63 ± 0.71a	13. 75 ± 1.61a	40.88 ± 1.59de	23.34 ± 0.81c
100	6.25 ± 0.72ab	14.13 ± 1.20a	37.79 ± 3.04cde	22.02 ± 1.43bc

Table 4

Average number of *A. craccivora* consumed by *A. exotica* at different densities.

** Life cycle not completed

Prey density	**Days**							**Total**
	1st instar (L1)		**2nd instar (L2)**		**3rd instar (L3)**			
	1st	2nd	3rd	4th	5th	6th	7th	
10	2.8 ± 0.49	6.2 ± 0.80	8.2 ± 0.66	9.8 ± 0.20	9.1 ± 0.30	9.7 ± 0.16	9.5 ± 0.27	**
30	2.2 ± 0.16	7.4 ± 1.25	9.5 ± 1.12	11.0 ± 0.98	24.9 ± 0.90	26.6 ± 1.65	28.1 ± 0.64	109.7 ± 5.70
40	2.4 ± 0.26	5.0 ± 0.93	6.6 ± 0.92	12.6 ± 1.99	25.5 ± 3.14	31.2 ± 2.24	37.2 ± 1.05	120.6 ± 5.27
50	3.2 ± 0.53	5.7 ± 0.84	8.9 ± 1.27	17.3 ± 1.87	33.5 ± 2.92	38.0 ± 2.31	35.6 ±3.98	142.1 ± 5.70
60	2.1 ± 0.23	6.5 ± 0.82	8.0 ± 0.60	16.7 ± 2.64	34.6 ± 3.97	43.0 ± 3.55	34.6 ± 5.4	145.6 ± 6.18
70	2.4 ± 0.18	5.9 ± 0.72	8.9 ± 1.16	16.4 ± 2.55	35.2 ± 2.85	48.0 ± 2.56	32.0 ± 4.63	149.7 ± 6.50
80	2.7 ± 0.25	10.5 ± 1.31	9.9 ± 1.13	17.6 ± 2.60	39.1 ± 4.08	45.1 ± 4.08	38.4 ± 4.4	163.4 ± 6.46
100	2.5 ± 0.19	10.0 ± 1.45	11.2 ± 1.36	17.0 ± 1.59	38.4 ± 4.1	41.0 ± 5.55	34 ± 5.23	154.1 ± 6.19

Table 5

Parameter estimates (attack rate and handling time) and summary of model selection analysis for the fits of four functional response models to different larval instars of *A. exotica.*

Model	**attack rate (*a*)**	**handling time (*h*)**		**SSQ**	**AIC**
First instar larvae (L1)					
Holling type II	0.089	4.473	$z = 1$	193.839	5.33
Holling type III	0.028	4.708	$z = 2$	196.466	5.35
θ-Sigmoid	0.107	2.48×10^{-6}	$z = 0.171$	184.431	5.32
Beddington-DeAngelis	0.143	4.473	$\gamma = 0.594$	193.839	5.37
Second instar larvae (L2)					
Holling type II	0.059	1.546	$z = 1$	767.866	**6.71**
Holling type III	0.009	1.845	$z = 2$	830.486	6.79
θ-Sigmoid	0.194	6.65×10^{-6}	$z = 0.251$	740.722	**6.71**
Beddington-DeAngelis	0.122	1.546	$\gamma = 1.074$	767.866	6.75
Third instar larvae (L3)					
Holling type II	0.249	0.538	$z = 1$	1396.711	7.31
Holling type III	0.023	0.597	$z = 2$	1380.707	**7.30**
θ-Sigmoid	0.063	0.581	$z = 1.577$	1369.247	7.33
Beddington-DeAngelis	0.387	0.538	$\gamma = 0.557$	1396.711	7.35
Larval stage (L1+L2+L3)					
Holling type II	0.076	0.872	$z = 1$	407.958	**6.08**
Holling type III	0.005	1.033	$z = 2$	431.871	6.14
θ-Sigmoid	0.043	0.931	$z = 1.219$	404.954	6.11
Beddington-DeAngelis	0.151	0.872	$\gamma = 0.974$	407.958	6.12

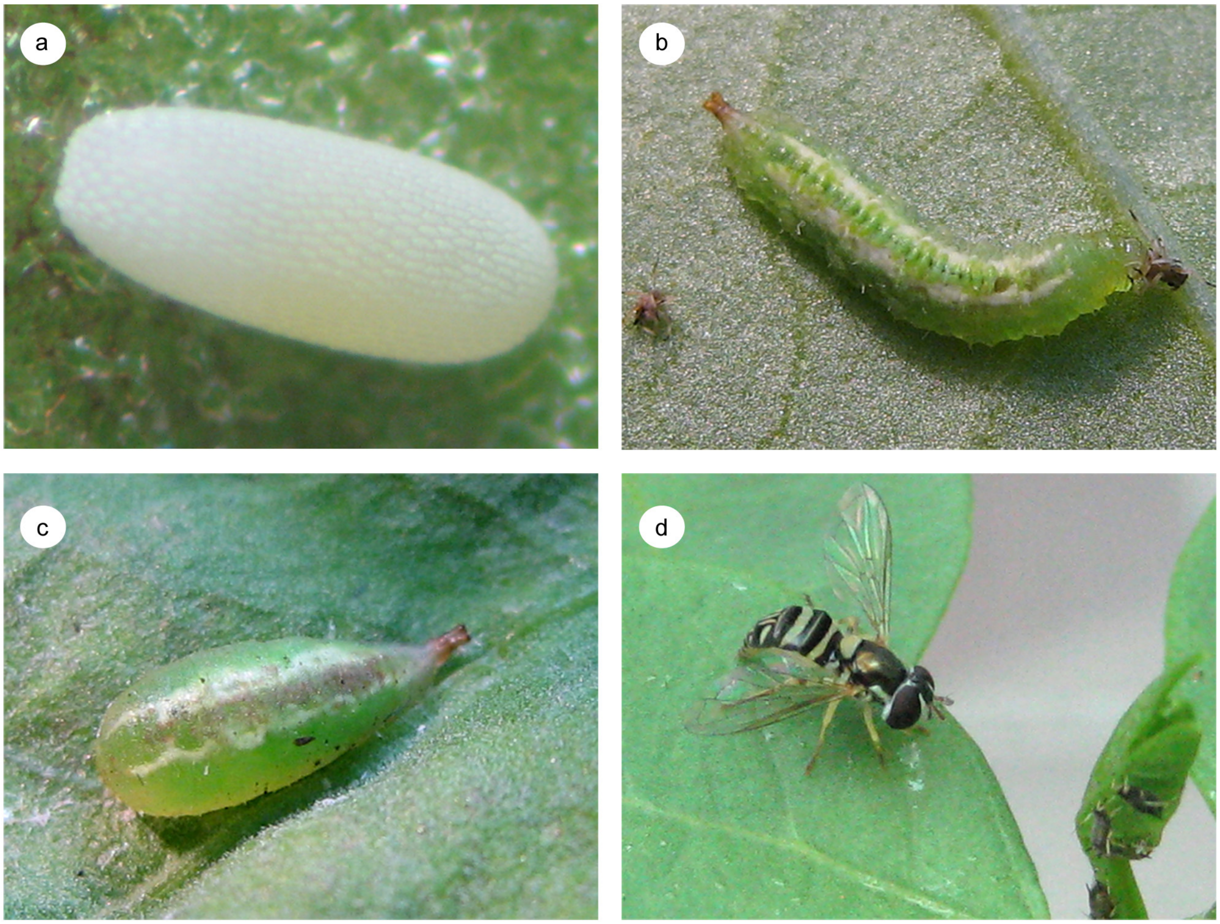
Figure captions

Fig. 1 Life cycle of the aphid predator *Allograpta exotica*: egg (**a**), third instar larva feeding on *Aphis craccivora* (**b**), pupa (**c**), female imago (**d**). Images by E. Arcaya.

Fig. 2 Survival rates of *Allograpta exotica* at 25 °C and 68% RH: the age-stage specific survival rate (*Sxj*) for each stage (**a**), and the age-specific survival rate (*lx*) for the cohort (**b**).

Fig. 3 The life expectancy (*exj*) of each age-stage group of *Allograpta exotica* at 25 °C and 68% RH.

Fig. 4 Functional response of first (**a**), second (**b**), and third (**c**) larval instars, and of the total larval stage (**d**) of *Allograpta exotica* to different densities of third and fourth instar nymphs of *A. craccivora*. The black dots represent the observed response and the lines are the predicted response by the four models.



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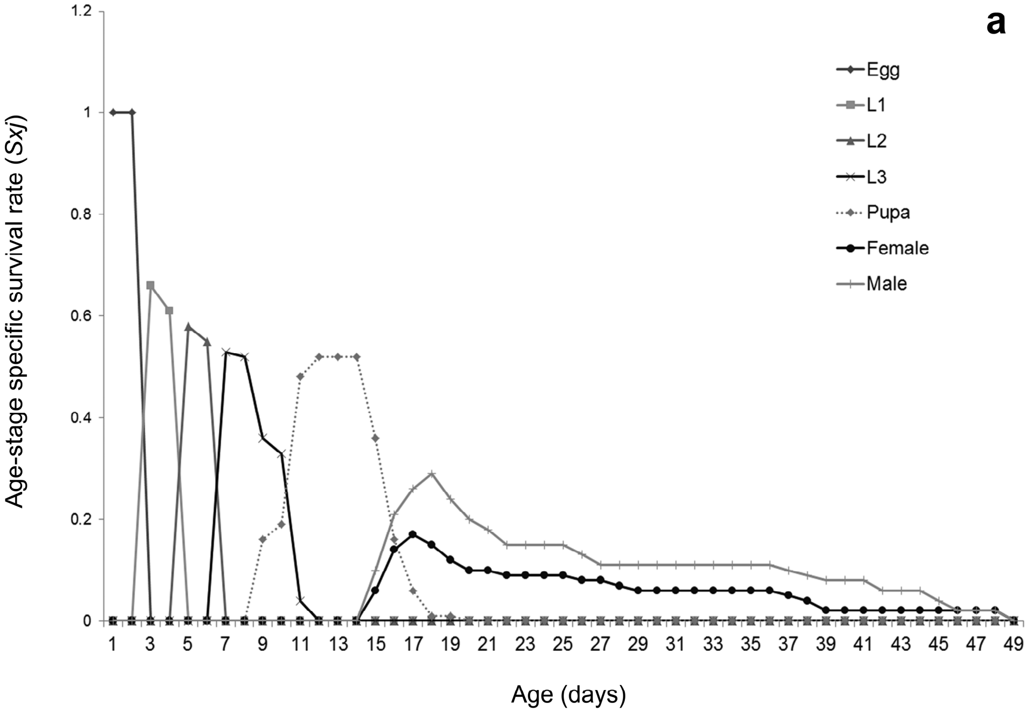
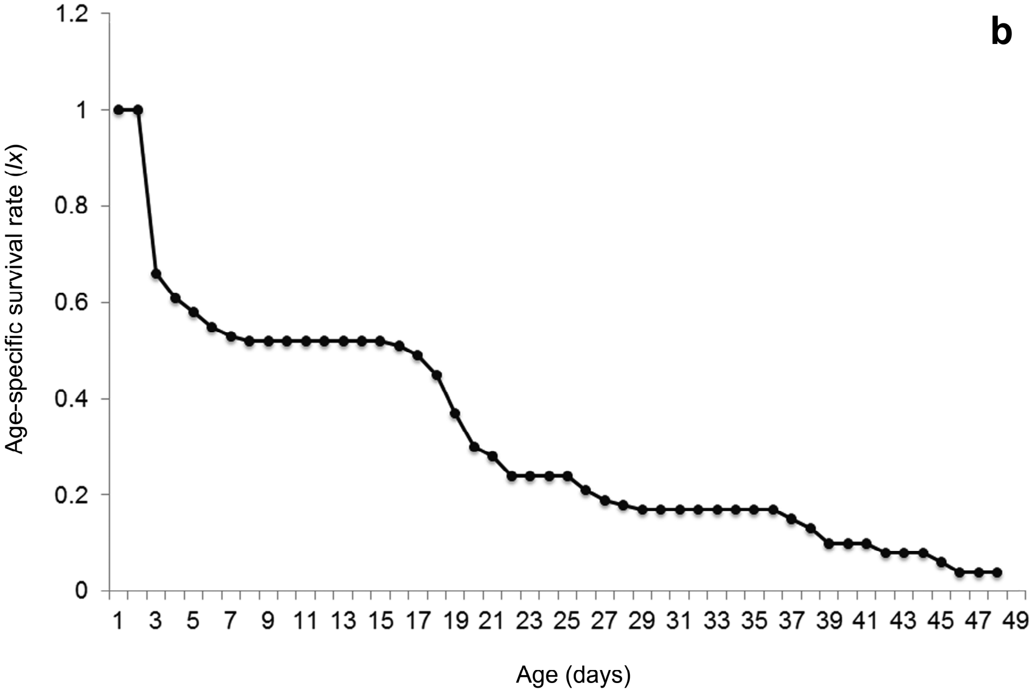
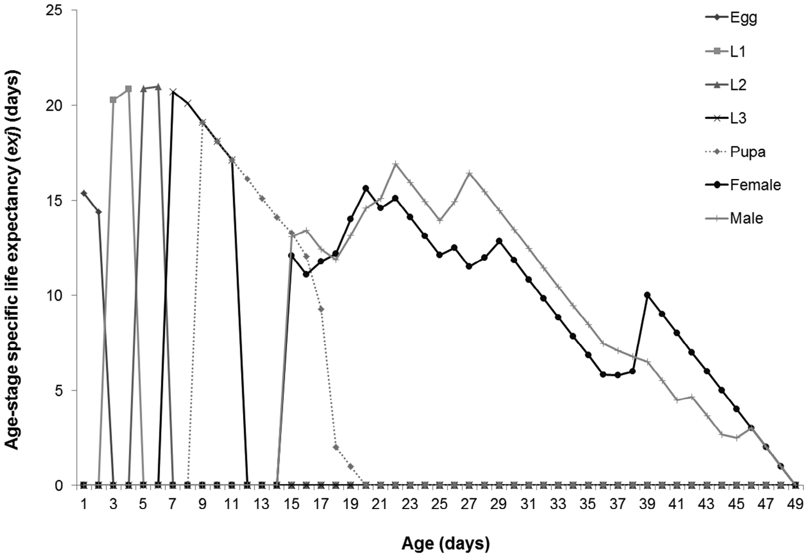
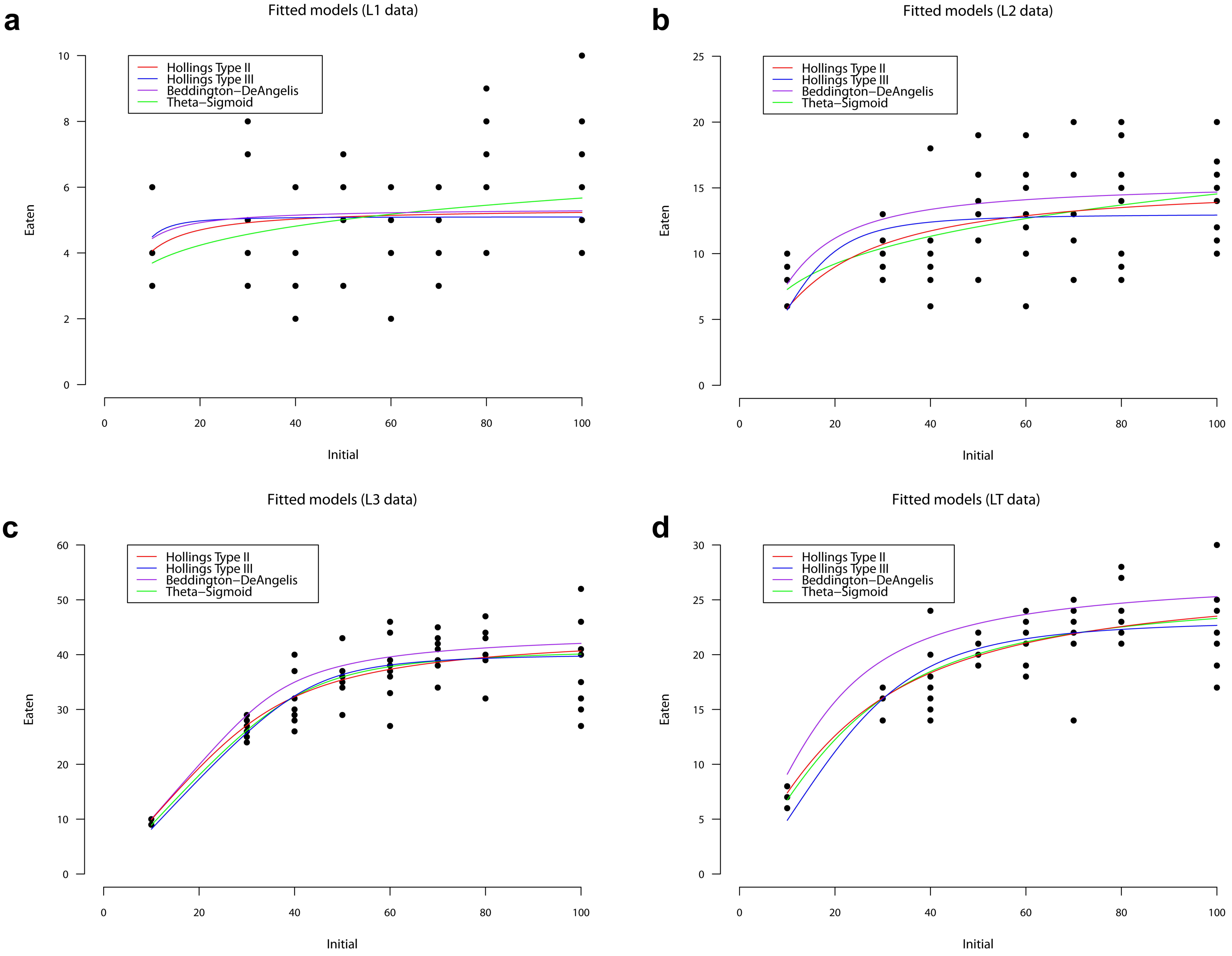

a
1.2
1
0.8
0.6
0.4
0.2
0
Age-stage specific survival rate (Sxj)
Egg
L1
L2
L3
Pupa
Female
Male
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45 47 49
Age (days)

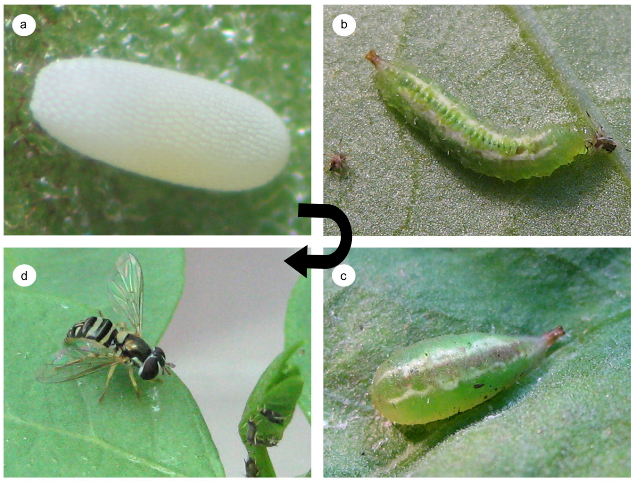

b
1.2
1
0.8
0.6
0.4
0.2
0
Age-specific survival rate (lx)
1 3 5 7 9 11 13 15 17 19 21 23 25 27 29 31 33 35 37 39 41 43 45 47 49
Age (days)

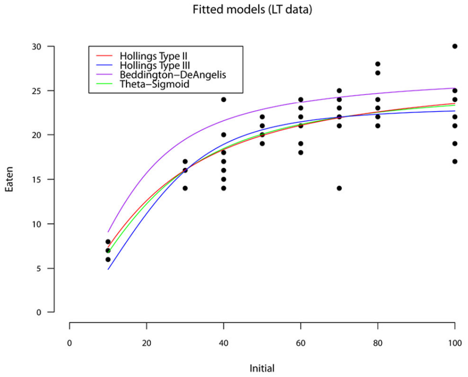

Age-stage specific life expectancy (exj) (days)
Age (days)
25
20
15
10
5
0
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
33
35
37
39
41
43
45
47
49
Egg
L1
L2
L3
Pupa
Female
Male


a
Fitted models (L1 data)
Hollings Type II
Hollings Type III
Beddington–DeAngelis
Theta–Sigmoid
Eaten
0
2
4
6
8
10
Initial
0
20
40
60
80
100
b
Fitted models (L2 data)
Hollings Type II
Hollings Type III
Beddington–DeAngelis
Theta–Sigmoid
Eaten
0
5
10
15
20
25
Initial
0
20
40
60
80
100
c
Fitted models (L3 data)
Hollings Type II
Hollings Type III
Beddington–DeAngelis
Theta–Sigmoid
Eaten
0
10
20
30
40
50
60
Initial
0
20
40
60
80
100
d
Fitted models (LT data)
Hollings Type II
Hollings Type III
Beddington–DeAngelis
Theta–Sigmoid
Eaten
0
5
10
15
20
25
30
Initial
0
20
40
60
80
100

Highlights

- Colonies of *Allograpta exotica* were successfully established in lab conditions
- The average duration of *Allograpta exotica* development was 15.04 days from egg to adult emergence
- Mortality rates observed during the larval stage decreased as larval development progressed
- The total number of prey consumed (from first to third instar larva) increased with increasing prey density, and handling time was shortest for the third larval instar
- Potential use of *Allograpta exotica* in augmentative biological control is proved


a
b
d
c


Fitted models (LT data)
Hollings Type II
Hollings Type III
Beddington–DeAngelis
Theta–Sigmoid
Eaten
0
5
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20
25
30
Initial
0
20
40
60
80
100