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Life cycle, population parameters, and predation rate of the hover fly *Eupeodes corollae* fed on the aphid *Myzus persicae*

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Abstract

To improve the effectiveness of biological control procedures, it is necessary to quantify the survival rate of a natural enemy through the various stages of the life cycle, the fecundity rate, and the predation rate from birth to death. It is not only important to obtain all the parameters associated with a life table, but also to quantify the predation rate in the life table framework. For this purpose, the life history, population parameters, and predation rate of *Eupeodes corollae* (Fabricius) (Diptera: Syrphidae) were determined using *Myzus persicae* (Sulzer) (Hemiptera: Aphididae) as prey and the age-stage, two-sex life table methods. As predators released in biocontrol programs are mass-produced from small populations with a consequent loss of genetic variability, we used specimens from a laboratory colony with similar characteristics. The highest mortality was found in the egg stage (54%). The mean developmental time of the pre-adult stage was 13.70 ± 0.08 days. In the adult stage, the mean longevity was 23.81 ± 1.14 days, with the males living longer than the females. The total preoviposition period was 17.62 ± 0.45 days and the mean female's fecundity was 169.81 ± 29.65 eggs per female. The population parameters indicated that the population grew with a net reproduction rate of 32.87 ± 7.25 offspring per individual and an average generation time of 23.05 ± 0.65 days. The values related to the number of aphid nymphs consumed by the larvae were: a mean predation rate (c_{xj}) of 485.20 ± 11.61 nymphs, a net predation rate (C_0) of 216.68 ± 16.89, and a finite predation rate (ω) of 28.03 ± 1.18. The results obtained support the use of *E. corollae* as valuable resource in the biological control of aphids, specifically *M. persicae*. Moreover, the technique implemented in this paper allows the objective comparison of *E. corollae* capacity as control agent with that of other aphidophagous hover fly species and other aphid's natural enemies.

Abbreviated abstract

The survivorship, reproduction, and predation rate of the aphidophagous hover fly *Eupeodes corollae* (Diptera: Syrphidae) fed on *Myzus persicae* (Hemiptera: Aphididae) were studied under controlled rearing conditions using a two-sex life table. According to the results, *E. corollae* can be considered a promising candidate for use in the biological control of aphids, specifically *M. persicae*, and the technique implemented allows the objective comparation of its capacity as control agent with other aphidophagous species.

Graphic for Table of Contents

Graphical abstract.png

Introduction

Hover flies (Diptera: Syrphidae) play an important role in agroecosystems by providing various ecosystem services such as the pollination of crops performed by adults and pest control carried out by the predatory larvae (Wotton, et al., 2019; Dunn et al., 2020; Pekas et al., 2020). Predatory larvae of most syrphines are known as generalist predators, feeding on aphids and other soft-bodied arthropods (Rojo et al., 2003; Rotheray & Gilbert, 2011). The potential of syrphid larvae as biocontrol agents is well known, especially for aphidophagous species (Agarwala et al., 1989; Tenhumberg & Poehling, 1995; Brewer & Elliott, 2005; Freier et al., 2007; Bugg et al., 2008; Pineda & Marcos-García, 2008; Haenke et al., 2009; Díaz et al., 2010; Hopper et al., 2011; Amorós-Jiménez et al., 2012, 2014; Sunil & Ballal, 2013; Arcaya et al., 2017; Fidelis et al., 2018). Three species are currently commercially produced in Europe. Two of them – *Episyrphus balteatus* (De Geer) and *Sphaerophoria rueppellii* (Wiedemann) – have been available for at least 8 years (van Lenteren, 2012; van Lenteren et al., 2018), and from 2020 *Eupeodes corollae* (Fabricius) became commercially available as well (Biobest, 2020).

Eupeodes corollae has been reported to prey upon at least 64 Aphididae species, but also some species of Thysanoptera and Lepidoptera (Rojo et al., 2003). In addition, its feeding strategy is considered by Cornelius & Barlow (1980) as 'energy maximizer' sensu Schoener (1971). This behaviour is desirable for a biocontrol agent because it ensures that throughout its predatory stage it will attack as many prey as possible even if it does not consume all the available biomass of the pest (Scott & Barlow, 1986). Its high predation potential is also applicable under greenhouse conditions (Hanzhong & Fang, 1992). Chambers (1986) shows that this species could be a suitable component of the integrated control of aphid pests resistant to chemical control on chrysanthemum and cucumber plants by combining its action with other natural enemies (e.g., with entomopathogenic fungi such as *Verticillium lecanii* R. Zare & W. Gams). The prey used in the experiment, the green peach aphid, *Myzus persicae* (Sulzer), is a serious pest of fruit trees and vegetables crops, being widely polyphagous and a vector of more than 100 plant viruses (van Emden et al., 1969; CABI, 2019). Due to its economic impact, knowledge about its natural enemies is crucial in order to develop efficient biocontrol programs.

One of the main tools used to quantitatively analyse the life history of insect populations in captivity and to compare the most important parameters of their controlled rearing is the life table methodology (Ning et al., 2017). Life tables summarize some of the main biological traits of the life cycle, such as survival and reproductive potential (fecundity), whereas the consumption rate

(predation rate in the case of predacious species) can be used to evaluate their preying capacity. This information is valuable for assessing the potential of the natural enemies in pest biocontrol programs. This demographic tool has become crucial in the development of artificial protocols related to the rearing under controlled conditions of insects used for pest control (Naranjo, 2001; Chi & Su, 2006; Ebrahimi et al., 2013; Madahi et al., 2013). Specifically, Chi & Liu (1985), Chi (1988), and Chi et al. (2020) developed age-stage, two-sex life table analysis by considering not only individuals and stages but also the fact that both sexes play an important role in population dynamics. In addition, a consumption-rate analysis based on the combination of the survival rate and the age-stage-specific predation rate of all the individuals in a population can also be included (Chi &Yang, 2003).

The preferred environment of the vagrant hover fly *E. corollae* is open ground. It is largely anthropophilic and can be found on most sorts of farmland (including arable land), suburban gardens, orchards, and parks (Speight, 2020). This species was one of the first predatory hover flies to be reared in captivity at laboratory scale (Bombosch, 1956, 1957), and consequently, a large amount of information about its life cycle, distribution and migration habits, larval development, larval feeding fitness and preferences, as well as larval competition with other species is available (e.g., Schneider, 1969; Rüzička, 1975, Barlow & Whittingham, 1986; Hågvar, 1974; Adams et al., 1987; Rojo et al., 1996; Putra & Yasuda, 2006; Pekas et al., 2020). Nevertheless, the main studies carried out on the life cycle and reproduction parameters of this species (e.g., Barlow, 1961; Benestad, 1970a,b) were performed using the traditional life table methodology, i.e., by referring only to female populations and ignoring the variable developmental rate among different individuals. This type of analysis often implies an unrealistic interpretation of the results (Chi & Liu, 1985; Chi et al., 2020).

The main aim of this study was to investigate the main biological parameters of the life cycle of *E. corollae*, compiling all the information needed to improve the commercial rearing and mass-production of this species. For this purpose, two specific objectives were set: (1) to record and analyse the developmental time of the various stages (egg, larva, pupa, and adult), the survival rate and fecundity, using the age-stage two-sex life table method; and (2) to analyse daily predation rates, using nymphs of the aphid *M. persicae* as prey.

Material and methods

Insect rearing

The prey used in the study were nymphs obtained from a colony of *M. persicae* belonging to the Department of Environmental Sciences and Natural Resources of the University of Alicante. The colony was maintained as a parthenogenetic laboratory culture fed on Italian sweet green pepper seedlings (*Capsicum annuum* L. var. *grossum*) in a rearing chamber at 20 ± 5 °C, 50 ± 10% r.h., and L16:D8 photoperiod, following the methodology of Ricci et al. (2000). The pepper plants were grown in polythene pots (9 × 9 × 10 cm) containing an industrial substratum composed of a mixture of black peat, perlite, lime, and inorganic nutrients (Compo Sana Universal; Compo Iberia, Barcelona, Spain) until they had at least 10 true leaves. The aphid culture was maintained by the addition of suitable plants once a week. Aphid-free plants were also grown to provide additional leaves for the Petri dish experiments.

As the predators released in biocontrol programs are mass produced in insectaries, the individuals obtained present loss of genetic variation and biological homogeneity due to some degree of domestication. For our work, we used specimens from a laboratory colony with similar characteristics by using a colony of *E. corollae* established from a total of nine wild adults (four males and five gravid females) collected from an almond tree field (Ibi, Alicante, Spain) in September 2018. The specimens were transferred to the laboratory in a plastic cage (22.5 × 14.5 × 13.5 cm) with a rectangular grille-type lid that prevents flies from escaping but allows proper air circulation. The cage used as transport device to the laboratory was provided with a piece of cotton soaked with water, a small container with ground white granulated sugar, and fresh pollen to ensure the flies' survival. After confirming the taxonomical identification of the specimens, they were sexed and transferred to a mesh rearing cage (40 × 40 × 40 cm), increasing the quantities of food and water, i.e., 10 g of fresh pollen, 10 g of ground white sugar, 9 ml of commercial honey, and a water dispenser. Food and water were replaced every 2 days.

As protein and carbohydrate sources, commercial foodstuffs used in human nutrition (honey and common sugar, i.e., sucrose) were used. As protein source, fresh pollen purchased from a local beekeeper was used. As an oviposition site, a 15-day-old pepper plant heavily infested with *M. persicae* nymphs was placed in the cage. The colony was maintained under the same abiotic rearing conditions used for the *M. persicae* colony. The pepper plants containing syrphid eggs (Figure 1A) were replaced daily and transferred to a rearing cage with the same characteristics as those of the adults' colony, containing six pepper plants infested with *M. persicae* nymphs for larval feeding. After pupation, the pupae were collected from the pepper plant growing substrate and from the recesses under the pots using soft tweezers to avoid damage.

The pupae were individually placed in 55-mm-diameter Petri dishes and again maintained in the above-mentioned rearing chamber until adult emergence. The adults obtained were sexed, and groups of 12 individuals (six females and six males) were transferred to other rearing cages to increase the number of specimens of the colony. The procedure was repeated over three generations in order to increase the colony and assure the species adaptation to the rearing conditions.

Morphological characterization of syrphid instars

In order to establish the duration of each instar of *E. corollae*, 75 newly hatched larvae were reared, and every 24 h 15 larvae were preserved in 70% ethanol, thus obtaining 24-, 48-, 72-, 96-, and 120-h-old specimens. The specimens were examined using a Leica MZ9.5 stereomicroscope (Leica Microsistemas, Barcelona, Spain) and each instar was determined following the morphological characters proposed by Benestad (1970a), i.e., size and colour of dorsal segmental sensilla and the distance between the two spiracular plates of the posterior respiratory process (prp). The first instars (L1) were distinguished by the presence of long black setae at the dorsal segmental sensilla and by the spiracular plates of the prp being clearly separated (Figure 1B). The second instars (L2) were characterized by the presence of stouter, light-coloured, or translucent segmental sensilla and by the spiracular plates of the prp remaining separated but closer than in the previous instar (Figure 1C). In the third instars (L3), the segmental sensilla remain without visible changes but the spiracular plates of the prp are fused (Figure 1D).

Life table and larval predation rate experiments

This study was performed in the above-mentioned rearing chamber under the same conditions used for the maintenance of the *E. corollae* and *M. persicae* colonies.

The life table and predation rate studies were carried out using the same individuals in order to prevent discrepancy and inconsistency between the data. The analysis started with a total of 217 *E. corollae* eggs (<12 h old) from the laboratory colony, that were transferred to rearing containers in groups of 10 eggs (except one with seven). Each container consisted of a 90 × 14 mm Petri dish filled with 15 ml of 3% agar-agar solution. The agar surface was covered with pepper leaves before it solidified, creating a leaf layer that conserves its turgidity and humidity for several days. This setup was similar to that used by Blande et al. (2004). A circular opening (4 cm diameter) was made in the Petri dish lid and was covered with a thin plastic mesh to maintain the

correct humidity and allow air circulation. Once the eggs were transferred, the containers were labelled according to the oviposition date and observed until hatching occurred. The neonates (Figure 1B) were placed individually in rearing containers and 25 *M. persicae* nymphs (3–4 days old) were added to each one using a thin, soft natural hairbrush. Finally, the container was labelled and sealed with laboratory film in order to prevent the larvae or aphids from escaping. After 24 h, the containers were opened and the surviving larvae were gently transferred to new rearing containers with 50 *M. persicae* nymphs, and these containers were sealed with laboratory film to prevent *M. persicae* nymphs from escaping. The number of *M. persicae* nymphs consumed was registered, as well as the number of dead *E. corollae* larvae. The procedure was repeated until pupation, increasing the number of aphid nymphs added each day (3rd day: 100 nymphs, 4th day: 150 nymphs, 5th day: 200 nymphs, 6th day: 250 nymphs, 7th day: 300 nymphs). The mortality of the aphids maintained in the Petri dishes was previously tested without the presence of syrphid larvae, being considered negligible as it was <0.5% in 24 h. Natural aphid mortality (not related to larval predation) was differentiated from mortality due to predation because aphid bodies remained complete with a dark brown/black colouration.

At the end of larval development, the pupae (Figure 1E) were individually transferred to 5-cm-diameter Petri dishes, labelled according to the pupation date, and observed until adult hatching. The date and sex of the adults of the cohort that emerged (i.e., 44 males and 42 females) was recorded. They were then placed in pairs (male-female) (Figure 1F) in plastic rearing cages such as the one described above for the collection of the wild adults. In the experiment, 42 pairs were formed. To avoid that the absence of mating could affect the percentage of fertilised eggs detected, the experiment was designed to exclude working with virgin females or females left alone after mating in case of premature male death. Then, the two males of the cohort that were not used to create the 42 pairs were used to replace the dead males of the experiments. In addition, females usually died before males, so it was not a problem to replace the males in the mating boxes as there were always enough individuals available. As a consequence, in all cases the females were paired with a male until their death. These cages were supplied with 2 g of fresh pollen, 4 g of sugar, 0.5 ml of honey, and a water dispenser. A 5-cm-diameter Petri dish with a leaf incrusted in agar with >20 *M. persicae* nymphs was used as an oviposition substrate. On a daily basis, the oviposition substrate was replaced, and the number of eggs laid by each female was recorded as well as the adults' death.

Life table analysis

For the life table analysis, the raw data obtained were processed using the TWOSEX-MSChart software (Chi, 2020a) and associated equations (Goodman, 1982; Chi & Liu, 1985; Chi, 1988; Burden & Faires, 2005; Chi & Su, 2006; Huang & Chi, 2012; Tuan et al., 2013). The life cycle parameters analysed were the age-stage-specific survival rate (s_{xj}) and the age-specific survival rate (l_x) (Table 1).

The fecundity parameters evaluated were the total preoviposition period (TPOP) of females, which is the time interval from egg hatching to the first oviposition of the individual; the adult preoviposition period (APOP) of females, which is the time elapsed from adult emergence to the first oviposition; the age-stage-specific fecundity (f_{xj}) that represents the number of eggs produced by each female individual of age x and stage j, the age-specific fecundity (m_x), and the age-specific maternity ($l_x m_x$) (Table 1). The population parameters calculated were the intrinsic rate of increase (r), the finite rate of increase (λ), the net reproductive rate (R_0), and the mean generation time (T). Finally, the age-stage life expectancy (e_{xj}) and the reproductive value (v_{xj}) were calculated following the equations detailed on Table S1.

Predation rate analysis

The raw data obtained on daily predation rates were analysed with the software CONSUME-MSChart (Chi, 2020b) and associated equations (Chi & Yang, 2003; Yu et al., 2005, 2013; Farhadi et al., 2011).

The parameters evaluated were the age-stage-specific consumption rate (c_{xj}) that represents the mean of aphids consumed by an individual of *E. corollae* at age x and stage j, the age-specific predation rate (k_x), the age-specific net predation rate (q_x), the net predation rate (C_0), which is the mean number of items of prey consumed by an average individual predator over its total life cycle, the transformation rate (Q_p), and finally the stable predation rate (ψ) and the finite predation rate (ω) (Table S2).

Statistical methodology

For the comparison between the sexes of the length of each instar, the complete larval stage, and the pupal and adult stages, the bootstrap paired test technique with $\alpha = 0.05$ was used (Efron & Tibshirani, 1993). In order to reduce the variability in means and standard errors when applying this technique, 10 000 replications were used in the analysis.

Results

Age-stage, two-sex life table study

Of the cohort of 217 *E. corollae* eggs with which the analysis started, only 46.1% successfully hatched 48 h after oviposition. Predation of newly hatched larvae on unhatched eggs was not detected. The mean developmental time of the larval stage was 5.6 ± 0.05 days (Table 1). Of the 100 individuals that emerged, only three died, during the second instar. The pupal stage, survived by 86 individuals, had a mean duration of 6.1 ± 0.05 days. Thus, the mean pre-adult stage of *E. corollae* lasted 13.7 ± 0.08 days. The pre-adult stage length of males and females did not differ significantly (Table 1).

Of the 86 adults that successfully emerged, 42 were female and 44 were male. Adult males lived about 10 days longer than adult females (28.9 ± 1.6 vs. 18.5 ± 1.2 days; Table 1). Overall, the complete life cycle of *E. corollae* took 37.5 ± 1.2 days (range: 15–69 days).

The age-stage survival rate (s_{xj}) curves indicated decreases over time and the biggest decrease was observed in the transition from the egg stage to the first instar, in accordance with the low percentage of egg hatch (Figure 2). These results were reflected too in the life expectancy (e_{xj}) curves, showing the lowest life expectancy in the egg stage ($E_{1,2}$ = 15.75), and the highest in the neonate larva (L1) ($E_{2,1}$ = 32.01) (Figure 3). Males showed a higher life expectancy and expected maximum longevity than females (69 vs. 51 days).

Although 42 females emerged, it was only possible to obtain reproductive parameters for 39 of them because three did not produce any eggs (Table 2). The total pre-oviposition period (TPOP) was 17.6 ± 0.5 days, whereas the adult preoviposition period (APOP) was 3.8 ± 0.5 days. In total, 7132 eggs were laid, ranging from three to 1188 eggs per female. The mean female fecundity (F) was 169.8 ± 29.6 eggs per female (including the females that laid no eggs), whereas the daily maximum fecundity was 136 eggs per female. The mean oviposition period lasted 9.8 ± 0.7 days, i.e., 52.9% of the female's life span (Table 2).

The contribution of an individual to the next generation is depicted in the age-stage reproductive value (v_{xj}) curves, typically showing that adult females make the maximum contribution (Figure 5). This contribution increased from day 13, when oviposition started, peaked on day 16 (v_{xj} = 69.62), and gradually decreased as the females aged, producing fewer eggs.

The population growth parameters of *E. corollae* indicated an intrinsic rate of increase (r) of 0.15 ± 0.01 and a finite rate of increase (λ) of 1.16 ± 0.01 per day (Table 3). The net

reproductive rate (R_0) was 32.87 ± 7.25 offspring per individual, and the mean generation time (T) was 23.05 ± 0.65 days.

Predation rate analysis

The total number of 3- and 4-day-old nymphs of *M. persicae* killed by the larvae of *E. corollae* throughout this study was 47019. The maximum consumption rate was 814 nymphs, and the maximum daily predation rate was 370 nymphs. The age-stage-specific predation rate ($c_{x,j}$) increased with the successive instars (Table 4, Figure 6). The consumption rate peaked on the 2nd day of the L3 instar (Figure 6). The average predation rate of males during the L1 and L2 instars was significantly higher than that of females (Table 4). During the L3 instar, when predation rate was highest, no significant difference was detected between the sexes (Table 4). The larval age-specific predation rate (k_x) and the age-specific net predation rate (q_x) increase from day 1 until day 6, then they drop steeply (Figure 7). The larvae stop feeding and empty their guts almost 24 h before pupation.

The finite predation rate (FP) was 28.0 ± 1.2 nymphs, and the net predation rate (C_0) was 216.7 ± 16.9 nymphs (Table 5). However, if only the 100 larvae that emerged are considered, instead of the initial number of eggs, the net predation rate of the effective consumer is 470.2 nymphs. Finally, the mean number of *M. persicae* nymphs needed to produce one *E. corollae* offspring, indicated by the transformation rate (Q_p), was 6.6 ± 1.5 nymphs/egg (Table 5).

Discussion

Life cycle

The egg to adult emergence period of *E. corollae* was 13.7 ± 0.08 days, close to that found by Benestad (1970a) also using *M. persicae* as prey. The length of the pre-adult stage with *M. persicae* as prey was substantially shorter than that obtained when other aphid species were used (Barlow, 1961; Pu et al., 2019). Factors that influence the life cycle length of *E. corollae* may be the rearing temperature and the size, number, and type of prey (Cornelius & Barlow, 1980; Hemptinne et al., 1993; Putra & Yasuda, 2006; Almohamad et al., 2009).

Although some studies have found that females live longer than males (e.g., Awadallah et al., 1980; Pu et al., 2019), Barlow (1961) found the opposite, as did we: the life span of males was 10 days longer than that of females. Further studies are needed to determine the origin of these differences and the possible effect of captive rearing in small boxes. Among these options, there

could be a relationship with the stress caused to females by the continuous mating attempts of males that can last for more than 2 h and during several days (Benestad, 1970a).

Survival rate and life expectancy

The main pre-adult stage mortality occurred during the egg stage – only 46.1% of the eggs hatched, similar to values obtained by Chambers (1986) and Barlow (1961). According to Chambers (1986), the high percentage of egg mortality could be the result of inefficient mating in captive rearing. This seems an unlikely explanation for our results, as the eggs were obtained from couples of *E. corollae* confined in small boxes, with long and frequent mating. Barlow (1961) observed that females laid fertile eggs in a high percentage one day but the next day none were fertile. We also found that females lay fertile and infertile eggs in the same clutch. We agree with Barlow that fertility may be dependent on sensory stimulation of the ovipositing female, which may influence the release of sperm from the spermatheca.

Benestad (1970a) found that hatching percentages depended on the rearing temperature, with the lowest percentage at 28 °C and the highest at 6 °C, so the eggs seem to tolerate rather extreme temperatures. In addition, she also reported that the viability of the eggs per female varies between 0 and 100% from one day to the next, but the differences were less than 30% when considering a period of several days. Wilkening (1961) observed the percentage of fertilized eggs in the field to vary with the season. More recently, Pu et al. (2019) reported an egg hatching rate of 92.5%. Considering all these results, more studies are needed to determine the causes of this variation in the rate of neonatal emergence in order to improve the rearing of this species under controlled conditions and use it in biocontrol programs.

Larval and pupal mortality was 3 and 14%, respectively. Barlow (1961) reported a higher larval mortality and a lower pupal mortality. In the adult stage, the mortality was more scattered, but most of the individuals died during the first 3 weeks (mainly females), although some males lived for almost 2 months.

The greatest life expectancy was found in the larval stage as a result of the high mortality in the egg stage. This was also found by Arcaya et al. (2017) for the Neotropical predatory syrphid *Allograpta exotica* (Wiedemann).

Reproductive parameters

The female maturation period is a key aspect in the mass production of insects and particularly

hoverflies (Campoy et al., 2020). The adult pre-oviposition period (APOP) of *E. corollae* in this study was extremely short compared with the 7-8 days usually required by predatory syrphids according to Sadeghi & Gilbert (2000) and other results obtained for *E. corollae* (Benestad,1970a; Scott & Barlow, 1984; Pu et al., 2019). One explanation for these differences could be the effect of the rearing temperature, which accelerates the maturation period when it is increased (Awadallh et al., 1980). This correlation has been reported in other fly species (e.g., Terblanche et al., 2005; Tochen et al., 2014; Li et al., 2015). The pre-oviposition period could be also affected by different adult diets (Dong et al., 2004).

The average number of eggs laid per female was very low compared with the values obtained in previous studies (Benestad, 1970a; Pu et al., 2019). These differences could be related to specific characteristics of the rearing systems such as the nutritional value of prey and the size of prey consumed by the larvae, the size of the imago isolation cages, the adult diet, and the abiotic conditions (Scott & Barlow, 1984; Dong & Xiong, 1988; Dong et al., 2004; Putra & Yasuda, 2006).

The reproductive value of females (v_{xj}) increased from day 13 reaching a maximum on day 16 after egg hatching. This parameter is key to its application in artificial rearing protocols for this species as it can be used to reduce the costs of maintaining adult colonies according to the number of individuals expected to be produced.

Population parameters

The mean generation time in this study was 23.05 ± 0.65 days, shorter than that reported by Barlow (1961) and Sharma & Bhalla (1995), who analysed the life table differently. In our work a shorter pre-oviposition period was observed as well. These values are the first obtained for this species using the two-sex life table methodology and can be used in a comparative analysis with different conditions or species of aphid as prey in order to improve the mass rearing of this predatory syrphid.

Predation rate

Although it is difficult to compare the larval consumption from different experiments involving different species and sizes of aphid as prey, some general trends are apparent. The number of aphids consumed by a larva increased considerably from one instar to another, regardless of the temperature. The mean aphid consumption of the L2 instar was almost 10× higher than that of the

L1, whereas the consumption of the L3 was 3× higher than that of the L2. There was little aphid consumption before the 3rd day (instars L1, L2), with < 90 aphids attacked per day. The predatory capacity increased from the 4th day and peaked on the 6th day after hatching, when the mean number of aphids consumed by the predators reached almost 160. The voracity decreased considerably during the last day before pupation. The same pattern was reported by Benestad (1970b), who used the same aphid, and by Pu et al. (2019) using *Aphis craccivora* CL Koch as prey.

The mean predation rate was 485.2 ± 11.6 aphids, although the net predation rate (C_0) was 216.7 ± 16.9 aphids, due to the fact that the non-hatched eggs were included in the calculation. As it is the pupae of *E. corollae* that are released in the field for biological control of *M. persicae*, the net predation rate should be considered to not underestimate the number of eggs required for effective pest control.

Based on the predation rate in this and earlier studies (Barlow, 1961; Barlow & Whittingham, 1986; Chambers, 1986; Putra and Yasuda, 2006; Pu et al., 2019), we consider that *E. corollae* is a promising candidate for use in the biological control of aphids, specifically *M. persicae*. Taking into account that *E. corollae* has recently become commercially available in Europe (BioBest, 2020), the use of the two-sex life tables methodology for the obtention of life cycle, fecundity, and predation values allows a realistic, clear, and objective comparison between the potential control capacity of *E. corollae* and other mass-produced aphidophagous species under similar conditions, or the control capacity of this hover fly under different conditions. This contributes to the choice of the most efficient agent for the biological control of aphids depending on the context.

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Figure captions

Figure 1 Life cycle stages of *Eupeodes corollae*: (A) egg, (B) first instar, (C) second instar, (D) third instar, (E) pupa, (F) adults mating.

Figure 2 Age-stage specific survival rate (s_{xj}) of *Eupeodes corollae*.

Figure 3 Age-stage life expectancy (e_{xj}) of (A) pre-adult and (B) adult *Eupeodes corollae*.

Figure 4 Age-specific survival rate (l_x) and fecundity parameters of *Eupeodes corollae*: age-stage fecundity (f_{i6}), age-specific fecundity (m_x), and age-specific maternity ($l_x m_x$).

Figure 5 Age-stage reproductive value (v_{xj}) of *Eupeodes corollae*.

Figure 6 Age-stage specific predation rate (c_{xj}) of *Eupeodes corollae* along the three larval instars of all individuals, whether they have reached the adult stage or not.

Figure 7 Age-specific survival rate (l_x), age-specific predation rate (k_x), and age-specific net predation rate (q_x) of *Eupeodes corollae*.

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1 Life cycle and fecundity parameters analysed using TWOSEX-MSChart software (Chi, 2020a).

Table S2 Predation parameters analysed using CONSUME-MSChart software (Chi, 2020b).

Table 1 Developmental time, adult longevity, and total longevity of *Eupeodes corollae* fed *Myzus persicae* nymphs

Parameters		n	Mean ± SE	Range
Developmental time (days)	Egg	100	2.00 ± 0.0	-
	First instar (L1)	100	1.00 ± 0.0	-
	Second instar (L2)	97	2.00 ± 0.0	-
	Third instar (L3)	97	2.60 ± 0.054	2-4
	Total larval stage	97	5.60 ± 0.050	5-7
	Pupal stage	86	6.07 ± 0.054	5-7
	Female pre-adult stage	42	13.81 ± 0.110a	13-15
	Male pre-adult stage	44	13.59 ± 0.110a	12-15
	Total pre-adult stage (both sexes)	86	13.70 ± 0.078	12-15
Adult longevity (days)	Female	42	18.52 ± 1.190x	4-37
	Male	44	28.86 ± 1.600y	2-55
	Adults (both sexes)	86	23.81 ± 1.143	2-55
Total longevity (days)	Female	42	32.33 ± 1.190	18-51
	Male	44	42.45 ± 1.640	15-69
	Adults (all individuals)	86	37.51 ± 1.150	15-69

Mean pre-adult and adult stages followed by the same letters are not significantly different (paired bootstrap test: P>0.05).

Table 2 Fecundity parameters of *Eupeodes corollae* females: total pre-oviposition period (TPOP), adult pre-oviposition period (APOP), fecundity, and mean oviposition days

Fecundity parameters	n	Mean ± SE
TPOP (days)	39	17.62 ± 0.452
APOP (days)	39	3.82 ± 0.462
Fecundity (F)	42	169.81 ± 29.648
Oviposition days (Od)	39	9.79 ± 0.718

Table 3 Population parameters of *Eupeodes corollae*

Population parameters	Mean ± SE
Intrinsic rate of increase, r (day^{-1})	0.152 ± 0.009
Finite rate of increase, λ (day^{-1})	1.164 ± 0.011
Net reproductive rate, R_0 (no. offspring)	32.866 ± 7.252
Generation time, T (days)	23.051 ± 0.649

Table 4 Mean (± SE; n in parentheses) predation rate (c_{xj}) of female and male L1, L2, and L3 *Eupeodes corollae* larvae

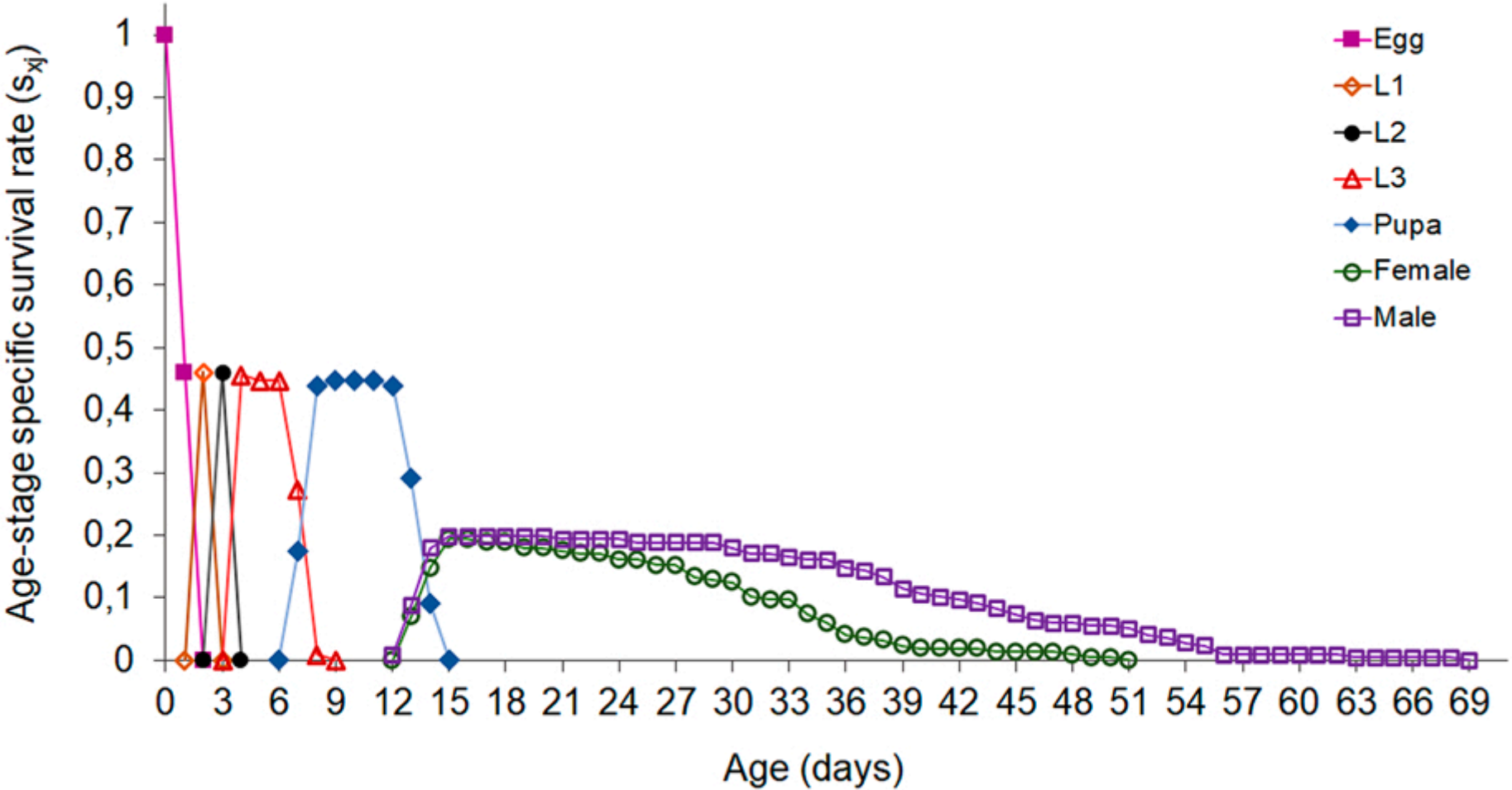
Parameter	Total population	Females	Males
First instar (L1)	11.91 ± 0.430 (100)	10.69 ± 6.480a (42)	13.30 ± 6.630b (44)
Second instar (L2)	115.45 ± 2.650 (100)	108.62 ± 6.480a (42)	120.05 ± 6.630b (44)
Third instar (L3)	354.21 ± 10.880 (97)	374.48 ± 6.480a (42)	343.66 ±6.630a (44)
Total larval stage	485.20 ± 11.610 (97)	493.79 ± 16.560 (42)	477.00± 16.370 (44)

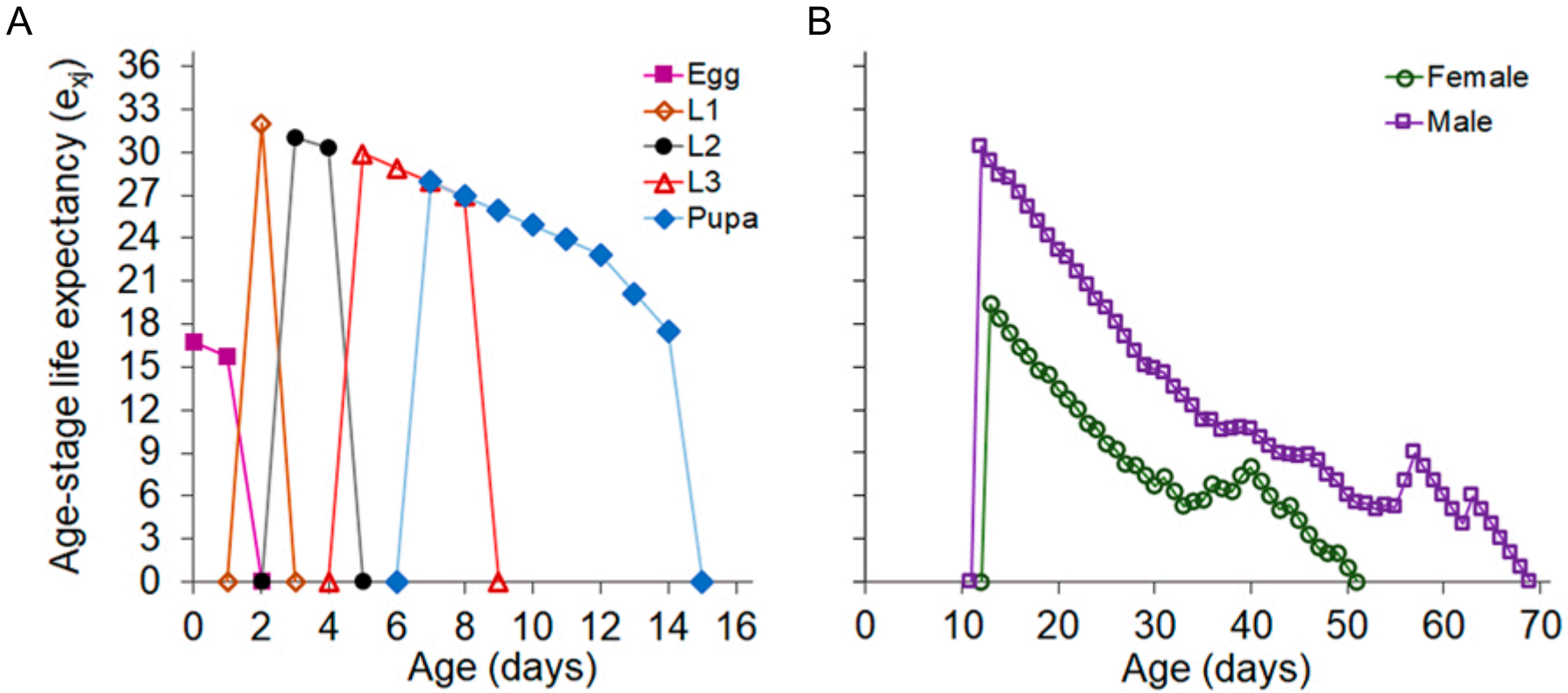
Means within a row followed by different letters are significantly different (paired bootstrap test: $P<0.05$).

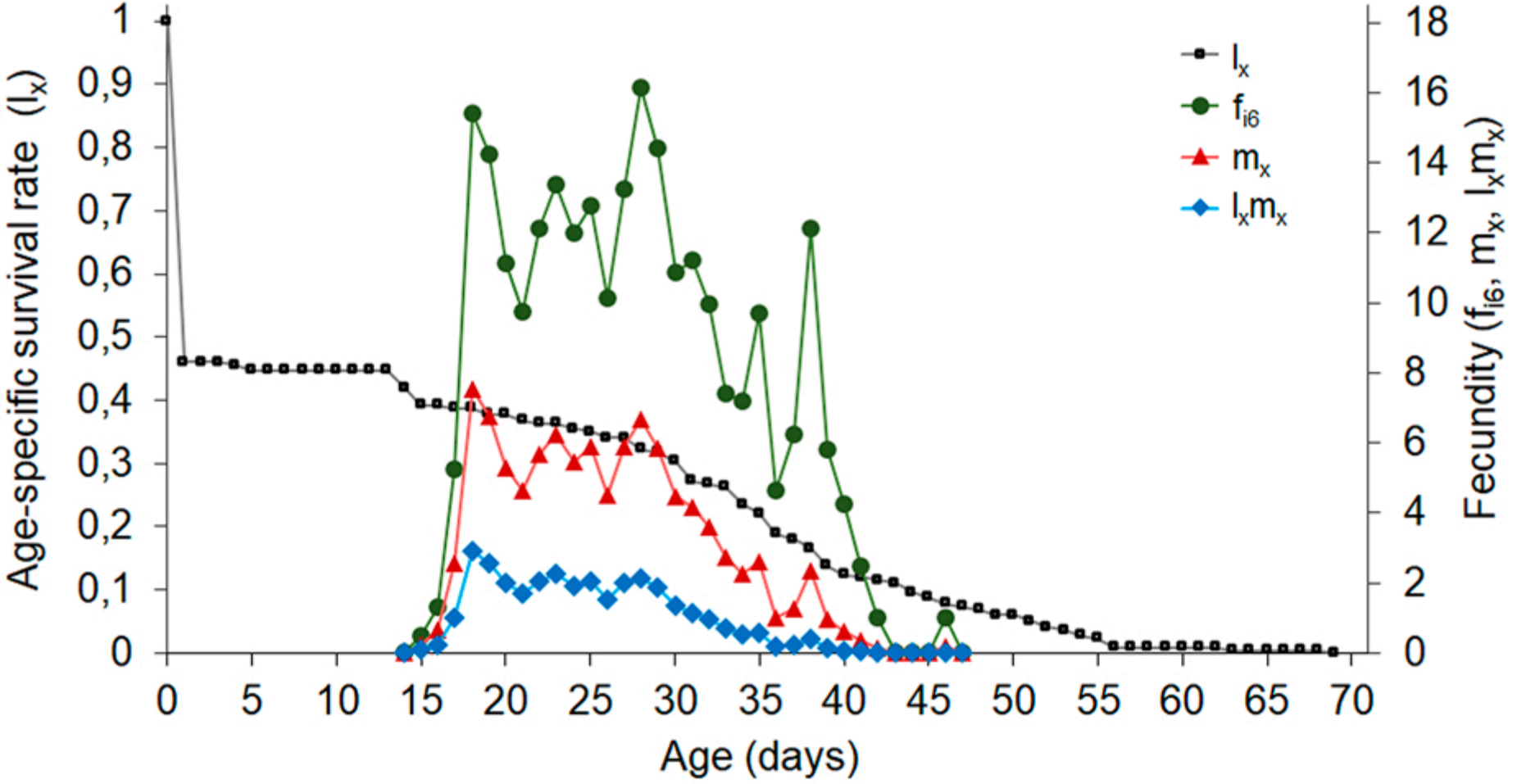
Table 5 Predation parameters for *Eupeodes corollae* fed *Myzus persicae* nymphs

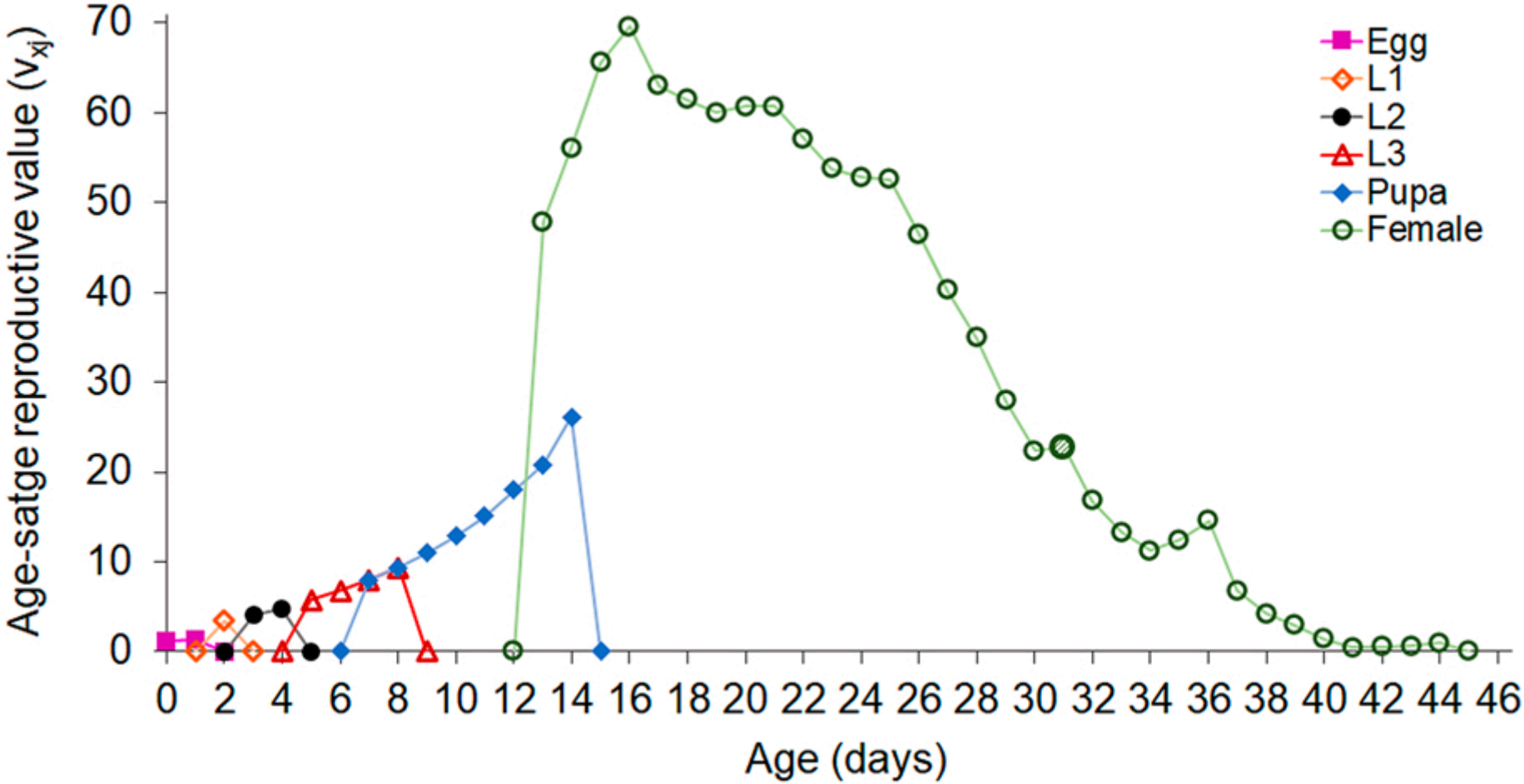
Parameter	Mean ± SE
Net predation rate, C_0 (nymphs)	216.677 ± 16.892
Finite predation rate, ω (nymphs)	28.031 ± 1.178
Transformation rate, Q_p (nymphs/offspring)	6.593 ± 1.509

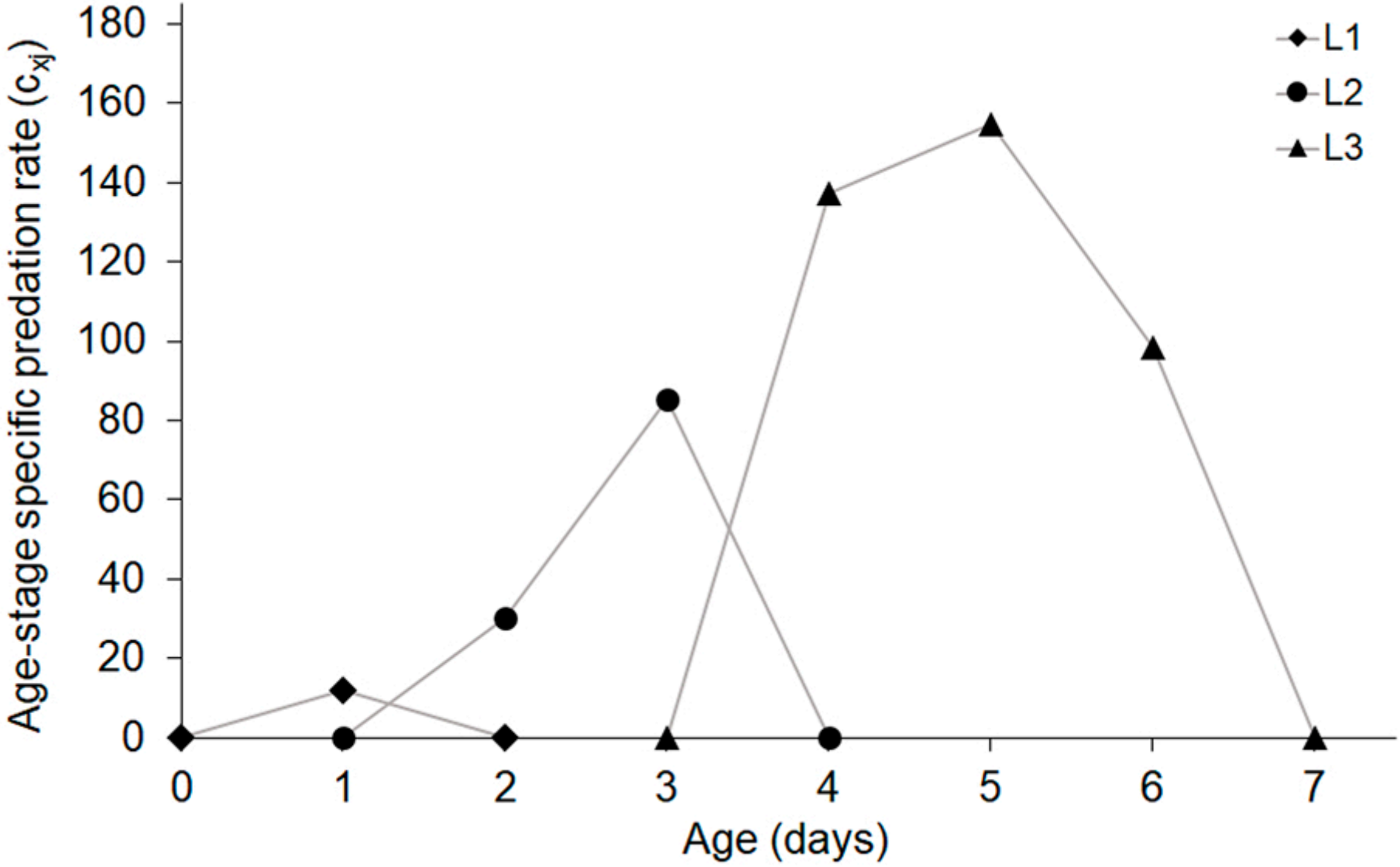

A
200 µm
B
200 µm
C
200 µm
D
1 mm
E
1 mm
F
1 mm

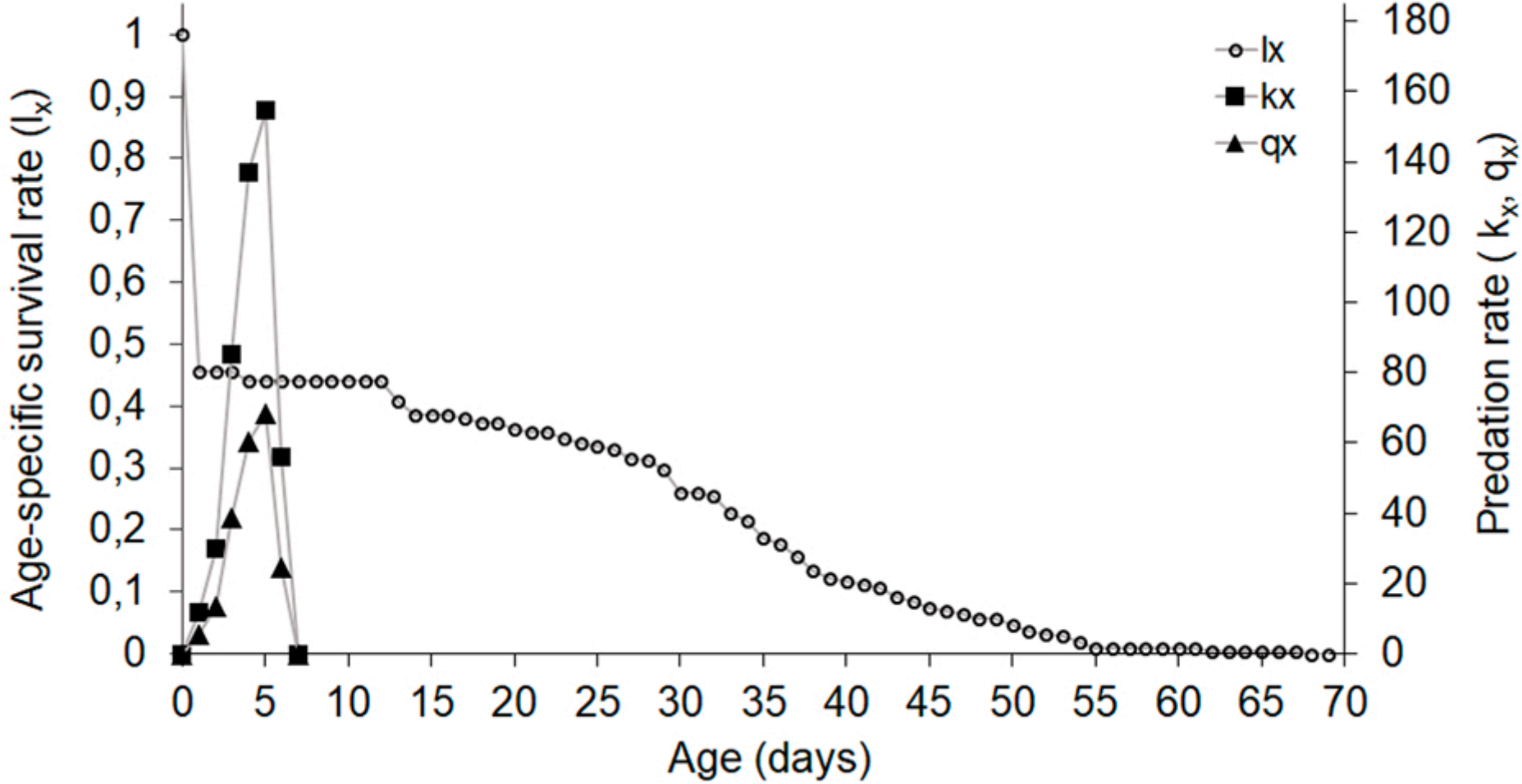

Age-stage specific survival rate (s_{xj})
1
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
0 3 6 9 12 15 18 21 24 27 30 33 36 39 42 45 48 51 54 57 60 63 66 69
Age (days)
Egg
L1
L2
L3
Pupa
Female
Male


A
Age-stage life expectancy (e_{xj})
36
33
30
27
24
21
18
15
12
9
6
3
0
0
2
4
6
8
10
12
14
16
Age (days)
Egg
L1
L2
L3
Pupa
B
0
10
20
30
40
50
60
70
Age (days)
Female
Male


Age-specific survival rate (l_x)
Fecundity (f_{i6}, m_x, l_xm_x)
Age (days)
l_x
f_{i6}
m_x
l_xm_x
0
0,1
0,2
0,3
0,4
0,5
0,6
0,7
0,8
0,9
1
0
2
4
6
8
10
12
14
16
18
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70


Age-satge reproductive value (v_{xj})
70
60
50
40
30
20
10
0
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32 34 36 38 40 42 44 46
Age (days)
Egg
L1
L2
L3
Pupa
Female


Age-stage specific predation rate (c_{xj})
180
160
140
120
100
80
60
40
20
0
0
1
2
3
4
5
6
7
Age (days)
L1
L2
L3


Age-specific survival rate (lx)
Predation rate (kx, qx)
Age (days)
lx
kx
qx
1
0,9
0,8
0,7
0,6
0,5
0,4
0,3
0,2
0,1
0
180
160
140
120
100
80
60
40
20
0
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70