



Life history traits and population growth of *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) local population from Serbia

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With 2 figures and 4 tables

Abstract: Life history traits (longevity, development time, parasitism rate and adult emergence) and population growth (instantaneous rate of increase) of six local populations of the parasitoid wasp *Encarsia formosa* Gahan, 1924, from several regions in Serbia (without a tradition in using commercial strains of the parasitoid for biological control of greenhouse whitefly) and the Dutch strain (D) were investigated in laboratory bioassays. The populations were reared on tobacco plants infested with greenhouse whiteflies *Trialeurodes vaporariorum* Westwood. The data acquired in the present study show that females of the local *E. formosa* population Bujanovac (B) showed most promising results for integrated control of whitefly in Serbia, with regard to their longevity and reproductive potential; the females B had the highest values of adult longevity in host absence (20.65 days), adult longevity in host presence (12.45 days), total parasitism (199.53 pupae/female), adult emergence (171.18 adults/female) and instantaneous rate of increase (0.240–0.303 day⁻¹). The life history traits of females B were significantly different from those of females in all other studied populations, except population D, for all parameters except longevity in host presence, and population Svilajnac (S), but only for adult longevity. Population S had the longest development time (15.70 days), significantly longer than all other populations (14.00–14.67 days), except population Zemun (Z) with 15.16 days. The females of local populations B, S, and the commercial population D had higher survivorship than those of the other four studied local populations. Our experiment provided initial data for further assessment of local populations of this parasitoid wasp as a biological agent to be used in control of greenhouse whiteflies in Serbia.

Keywords: biological control – *Encarsia formosa* Gahan, 1924 – development – reproduction – population growth

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1. Introduction

The greenhouse whitefly *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) is a cosmopolitan and highly polyphagous pest species of greenhouse crops, especially tomato (Gerling 1990). The native range of *T. vaporariorum* is not known, but it is assumed to be North or South America (CABI 2013). It has been widespread in Serbia since the 1970s (Zahradnik 1963) and frequently found in greenhouses as one of the most serious pests of vegetables and ornamentals (Perić 1999, Prijović et al. 2014). Apart from the immediate damage that its adults and larvae make by sucking cell saps from plant phloems and by secreting honeydew, the species also causes indirect damage as a vector of some plant viruses (Wisler et al. 1998, Brødsgaard & Albajes 1999, Martin et al. 2000). The greenhouse whitefly is also a vector of the broad mite *Polyphagotarsonemus latus* Banks, another serious pest of several greenhouse crops worldwide, which has also been observed in Serbia (Palevsky et al. 2001, Petanović et al. 2010).

The use of chemical insecticides, which is still the main approach to control of this pest, has caused whitefly resistance to compounds of earlier generations, as well as to neonicotinoids and other newer insecticides (Gorman et al. 2001, 2007, Karatolos et al. 2010, Whalon et al. 2014). The situation therefore requires long-term and sustainable strategies for controlling this pest species that should be based on an integration of chemical, biological, cultural and other measures (van Lenteren & Martin 1999, Gentz et al. 2010, Prijović et al. 2012).

A large number of parasitoids of whiteflies and scale insects belong to the genus *Encarsia* (Hymenoptera: Aphelinidae) (Gerling 1990). The parasitic wasp *Encarsia formosa* Gahan has been used for many years for biological control of *T. vaporariorum* as one of the most successful biological agents in greenhouse and ornamental crops around the world (van Lenteren & Woets 1988, van Lenteren et al. 1997, Pilkington et al. 2010). *E. formosa* females are the uniparental, primary parasitoids of greenhouse whiteflies, while males rarely occur. Females prefer to oviposit in third- and fourth-instars and prepupal nymphs of the host (Gerling 1990, Hoddle et al. 1998). Wasps of the genus *Encarsia* are the most important parasitoids of greenhouse whiteflies identified in Serbia. Four species of *Encarsia* have been detected in Serbia: *E. formosa*, *Encarsia tricolor* Foerster, *Encarsia partenopea* Masi and *Encarsia lutea* Masi. *E. formosa*, the most widespread of the four, has been observed as a parasitoid of *T. vaporariorum* and *Aleyrodias lonicerae* Walker on cucumbers, tomatoes, beans, painted daisies, geraniums, chrysanthemums and some other ornamentals, and on nettle and many other species of wild flora (Perić 1999).

Many studies focusing on different aspects of the biology of a highly commercialized Dutch strain of *E. formosa* have been published so far (Speyer 1927, Stenseth 1977, Kajita & van Lenteren 1982, Arakawa 1982, Bethke et al. 1991, Szabo et al. 1993, Donnell & Hunter 2002). According to Němec & Starý (1984), the origin of the Dutch (Koppert B. V) strain was from Glasshouse Crop Research Institute Littlehampton- GCRI, who's material came "from the original culture brought to the GCRI from Chesthunt (Great Britain) in the early 1920s and maintained here ever since (G. Grimmett)". They classified this population as the "historical standard".

On the other hand, there have been few studies of the parasitoid's local populations reared on whitefly hosts (Vet & van Lenteren 1981, Henter & van Lenteren 1996, Hu et al. 2002, Grill et al. 2012). In the present study, life history traits of six local populations of *E. formosa* originating in different regions of Serbia were examined and compared to the Dutch strain.

As implementation of the principles of integrated control of whiteflies is in its initial stage in Serbia at present, data on the parasitoid potentials of those local populations were intended to create a starting point for further research that would focus on improvement of local whitefly management programmes.

2. Materials and methods

2.1. Origin and rearing of parasitoids

The local populations of *E. formosa* were set up from pupae collected in tunnel greenhouses of vegetables and ornamentals and surrounding weeds, in localities without a tradition in using commercial strains of the parasitoid for biological control of greenhouse whitefly. By the beginning of the collection pupae, the Dutch strain of *E. formosa* has been used for biological control of three commercial greenhouses in northern Serbia, hundreds of miles away from the nearest locations from which were collected parasitoid local populations that were used in this study. Table 1 gives information on place of collections, the host species, host plant, and the number of parasitoids used to start the culture.

The local populations were established from parasitoids collected at the pupae stage and isolated in gelatin capsules until adult emergence. The emerged female wasps of each population were identified as *E. formosa* according to guide for identification given by Polaszek et al. (1992). After identification, the rest of the adults that emerged from each local population were vented into cages containing third and fourth stage larvae of whitefly in order to multiply. The multiplied wasp populations followed the pattern of asexuality that had been observed in other studies of *E. formosa* (Zchori-Fein et al. 1992), males were produced at very low frequency under normal rearing conditions. The Dutch strain of *E. formosa* (*E. formosa* D.) was purchased from Zeleni hit d.o.o., the Serbian agent of Koppert Biological Systems Inc., The Netherlands and successfully cultured as a reference strain.

Table 1. The local populations of *Encarsia formosa* Gahan, 1924 (Hymenoptera: Aphelinidae) from Serbia.

Locality	GPS coordinates	Population abbreviation	Whitefly host plant	The number of collected pupae ♀
Bujanovac	42°30'27" N, 21°48'30" E	B	<i>Solanum nigrum</i> L.	75 ♀
Mršinci (Čačak)	43°48'17" N, 20°29'30" E	M	<i>Cucumis sativus</i> L.	82 ♀
Negotin	44°13'00" N, 22°31'00" E	N	<i>Hibiscus</i> sp.	63 ♀
Pirot	43°07'476" N 20°19'13" E	P	<i>Pelargonium</i> sp.	116 ♀
Svilajnac	44°14'10" N, 22°40'31" E	S	<i>Lycopersicon esculentum</i> Miller	89 ♀
Zemun	44°50'43" N, 20°24'37" E	Z	<i>Nicotiana tabacum</i> L.	105 ♀

The Dutch strain of *E. formosa* and six local populations of this parasitoid wasp have been reared on *T. vaporariorum* hosts at 27 ± 1 °C and $60 \pm 10\%$ R.H. with a 16L: 8D h photoperiod. The population of *T. vaporariorum* was set up in 2008 from insects collected from tobacco plants in an experimental plastic greenhouse in Zemun. Whiteflies have been reared massively on tobacco plants, cv. Samsun, in ventilated muslin cages (100 cm × 60 cm × 40 cm). In this experiment, 21–24 tobacco plants were placed into each cage for whiteflies to lay eggs. Two or three days later, whitefly adults were blown back into cages and the plants taken out and kept in separate cages until the third or fourth instar of host nymphs have developed. Tobacco plants with the host insects were moved during that development stage to smaller cages (40 cm × 40 cm × 30 cm) to enable parasitism of adult wasps of different populations. By starting every new colony with pupae and keeping different populations in different rooms, contamination of local parasitoid cultures by each other and the Dutch strain was prevented. Two days later, plants with parasitized hosts were taken out, while parasitoid adults were blown back into cages. Parasitized pupae were collected after 18 days.

2.2. Bioassays

All bioassays were carried out under 27 ± 1 °C, $60 \pm 10\%$ R.H. and 16L: 8D h photoperiod with four replications. A bioassay for comparing the development times was conducted on tobacco plants around three weeks old and up to 30 cm high. All other bioassays were performed in Petri dishes (12 cm diameter), each having four (1 cm Ø) lid openings with muslin covers on top to provide ventilation and prevent internal condensation.

2.2.1. Development time

To determine the time of development, five females of *E. formosa* in perforated plastic bags were released by fixing each bag around a petiole of a tobacco leaf infested with 120–150 fourth-instar whitefly nymphs. After 24 h, the females were removed together with bags. When parasitoids were on the verge of emerging from pupae, 12 h counts were made of the number that had emerged (Enkegaard 1993). The development time was calculated as the total number of days from the parasitoid's egg laying to adults emerging from pupae. The data were transformed by \sqrt{x} and analyzed by a one-way ANOVA with the means separated by Fisher's LSD test ($p < 0.05$) (StatSoft, version 7).

2.2.2. Adult longevity

Batches of 20 females of *E. formosa* aged up to 24 h were used in the longevity bioassay. Longevity without host was measured in Petri dishes containing only a few droplets of honey. Longevity with host was measured in Petri dishes, each containing a layer of 1% agar upon which a leaf was placed that was infested with 250–350 third- or fourth-instars of *T. vaporariorum* nymphs (Qiu et al. 2004). Two or three days later, females were transferred to new Petri dishes with hosts, and the transferring continued until the death of the last insect. The number of females alive was checked daily in both variants. Adult longevity was calculated as the total number of days that each female lived, assuming that females died at the midpoint of 24 h interval. The Kaplan-Meier analysis was used to estimate longevity data (SPSS Statistics, Version 17) and survival curves (StatSoft, version 7). The longevitys of different populations were compared using one-way ANOVA with the means separated by Fisher's LSD test ($p < 0.05$). The log-rank test was applied to compare survival rates (StatSoft, version 7).

2.2.3. Parasitism and population growth

Ten females of *E. formosa*, aged up to 24 h, were placed in each Petri dish containing a 1% agar layer upon which a tobacco leaf was placed carrying 250–350 whitefly third- or fourth-instar nymphs. After 48 h, live females were transferred to new leaves with host nymphs and transferring continued until the last female died (Stouthamer & Mak 2002). The number of parasitized hosts was determined when nymphs changed color from light to dark. After counting, parasitized (black) pupae were transferred to new Petri dishes to monitor the emergence of adult parasitoids.

Parasitism was calculated as the number of parasitized pupae per female alive at the midpoint of 48 h (parasitization rate) and summed over the female lifetime (total parasitism). Adult emergence was calculated as a total number of individuals reaching the adult stage from parasitized pupae. Parasitism and adult emergence data were transformed by $\sqrt{(x + 0.5)}$. Data were analyzed by a one-way ANOVA and the means separated by Fisher's LSD test ($p < 0.05$).

The theoretical population growth was estimated by the instantaneous rate of increase (r_i) with the following equation:

$$r_i = [\ln (N_t/N_0)]/\Delta t$$

where N_0 is the initial number of individuals (ten adult females per replicate), N_t is the number of individuals at the end of t^{th} day (the number of surviving adult females, black (parasitized) pupae and adults emerged), and Δt is the number of days elapsed between the start of the bioassay and the end of t^{th} day. The individuals were counted at the end of the 16th, 18th and 20th day after the start of oviposition. Positive r_i values indicate a growing population, negative r_i values indicate a population in decline and $r_i = 0$ indicates a stable population (Walthall & Stark 1997, Vargas et al. 2002). Calculated r_i values were analysed by one-way ANOVA, and the means were separated by Fisher LSD test ($p < 0.05$).

3. Results

3.1. Development time

First adults of all *E. formosa* populations started their massive emergence on the 14th day after egg laying began, and their development mostly completed by the 18th day. In *E. formosa* populations D, S and P, some of the juveniles developed for 21 days. Statistically significant differences between populations were detected regarding the duration of juvenile development ($F_{6,21} = 4.55$, $p < 0.01$). The longest juvenile development was found in *E. formosa* population S (15.70 ± 0.23 days), significantly longer than in populations M (14.00 ± 0.13 days), B (14.40 ± 0.13 days), N (14.56 ± 0.41 days), P (14.63 ± 0.21 days) and D (14.67 ± 0.39 days). In population Z, juvenile development was 15.16 ± 0.12 days and it was significantly longer than the development of populations M and B.

3.2. Adult longevity

Fig. 1 presents adult longevity of *E. formosa* females in the presence and absence of host. Adult longevity was considerably shorter (1.26–1.40 times) in the presence of host in all studied populations. When a host was not offered for parasitism, the female longevity of population B (20.65 days) was significantly longer statistically than it was in populations Z, M, P and N, and it was not significantly different from the longevity of females in populations S and D ($F_{6,21} = 13.099$, $p < 0.001$). In host presence, the females of population B lived statistically significantly longer (12.45 days) than all other females, except females in population S ($F_{6,21} = 16.847$; $p < 0.001$). Females from populations S lived significantly longer (11.81 days) comparing to all other local populations, but not significantly longer than commercial females D (11.20 days). In both variants, females of population N lived significantly shorter than all other females.

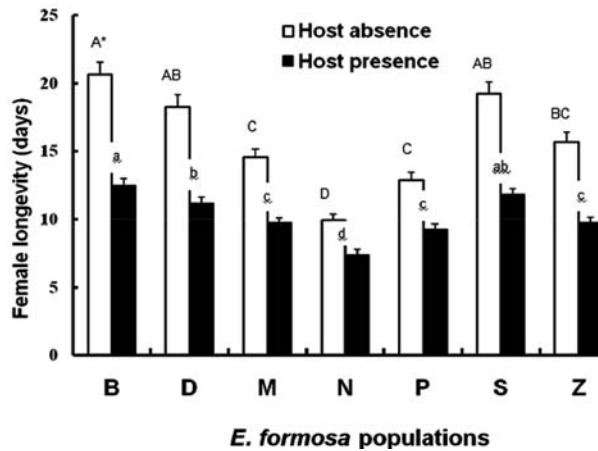


Fig. 1. Adult longevity (means \pm SE) of *Encarsia formosa* Gahan, 1924 (Hymenoptera: Aphelinidae) females from local populations Bujanovac (B), Mršinci (M), Negotin (N), Pirot (P), Svilajnac (S) and Zemun (Z), and the Dutch strain (D), in the presence and absence of the host, third- or fourth-instar of *Trialeurodes vaporariorum* nymphs.

* the mean values with different letters above rectangles differ significantly (ANOVA followed by Fisher LSD test, * $P < 0.05$). Capital letters mark differences in longevity in host absence, lower-case letters mark differences in host presence

The survival curves of the examined *E. formosa* populations are shown in Fig. 2. In host absence (Fig. 2A), females from population B had higher survivorship than those from populations M (ww = -31.13, $p < 0.001$), Z (ww = -25.07, $p < 0.001$), N (ww = -37.67, $p < 0.001$), and P (ww = -36.31, $p < 0.001$). The same was found for the survival of females from population S (S vs. M: ww = -25.84, $p < 0.001$; S vs. Z: ww = -18.07, $p < 0.01$; S vs. N: ww = -35.27, $p < 0.001$; S vs. P: ww = -32.64, $p < 0.001$) and population D (D vs. M: ww = -24.87, $p < 0.001$; D vs. Z: ww = -16.87, $p < 0.01$; D vs. N: ww = -33.87, $p < 0.001$; D vs. P: ww = -32.15, $p < 0.001$). There were no significant differences among the females of populations B, S, and D. The females from populations N and P had the lowest survivorship that differed significantly from all other females, and a significant difference was detected between the two (N vs. P: ww = 20.27, $p < 0.001$). In host presence (Fig. 2B), higher female survivorship was found in population B (B vs. M: ww = -22.64, $p < 0.001$; B vs. Z: ww = -3.87, $p < 0.001$; B vs. N: ww = -33.46, $p < 0.001$; B vs. P: ww = -24.46, $p < 0.001$), population S (S vs. M: ww = -18.97, $p < 0.001$; S vs. Z: ww = -17.18, $p < 0.001$; S vs. N: ww = -33.00, $p < 0.001$; S vs. P: ww = -20.72, $p < 0.001$) and population D (D vs. M: ww = -15.57, $p < 0.01$; D vs. Z: ww = -13.75, $p < 0.01$; D vs. N: ww = -30.24, $p < 0.001$; D vs. P: ww = -17.47, $p < 0.001$). No significant differences in survival were detected among the females of these three populations. The females from population N had the lowest survivorship, significantly different to the other females.

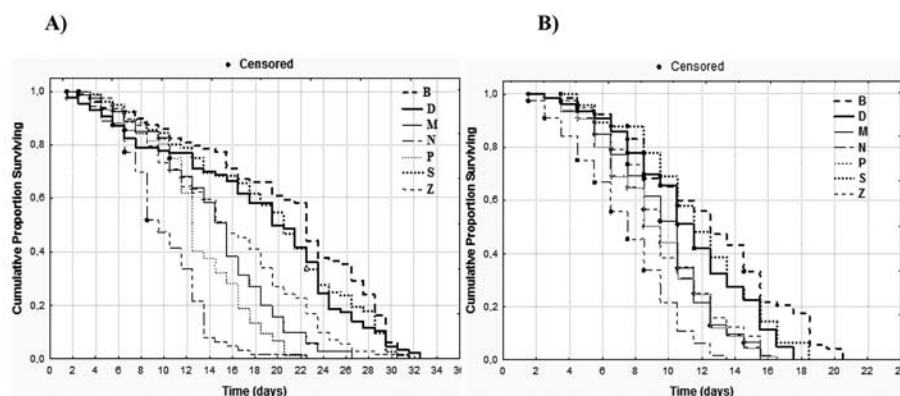


Fig. 2. Survival curves of *Encarsia formosa* Gahan, 1924 (Hymenoptera: Aphelinidae) females from local populations Bujanovac (B), Mršinci (M), Negotin (N), Pirot (P), Svilajnac (S), Zemun (Z) and the Dutch strain (D) in the absence (A) and presence (B) of the host, third- or fourth-instars of *Trialeurodes vaporariorum* nymphs.

3.3. Parasitism and population growth

Parasitization rates of the examined *E. formosa* populations are shown in Table 2. In our experiment, females of the examined populations in the initial six days of oviposition parasitized up to 52% of all parasitized pupae. Maximal parasitization rates were recorded on the third and fourth days of oviposition, from 20.38 pupae/female/48h (population M) to 28.85 pupae/female/48h (population B). Over the following four days, parasitization rates were high and then started to decline. Over the initial 14 days, which is a period corresponding to the shortest oviposition interval (population N), the highest parasitization rates were found in females from populations B and D.

The examined *E. formosa* populations showed statistically significant differences in total parasitism ($F_{6,21} = 16.41$, $p < 0.001$) and adult emergence ($F_{6,21} = 13.81$, $p < 0.001$) (Table 3). The highest values of those two life history traits, found in females from populations B (199.53 pupae/female and 171.18 adults/female) and D (183.25 pupae/female and 159.58 adults/female), were significantly different from those of females in the other populations (all except population S). Females in population N had the lowest values of total parasitism and adult emergence, which were 36% and 34% lower than in females from population B. These parameters were not significantly different in females from populations M and N.

When total parasitism and adult emergence were calculated for a period of 14 days (to cancel the effect of different oviposition duration), those parameters in females of population B (163.18 and 133.04) and D (162.25 and 141.74) still had significantly higher statistical values than females in all other populations ($F_{6,21} = 19.00$, $p < 0.001$; $F_{6,21} = 12.39$, $p < 0.001$).

Table 2. Parasitization rates (means \pm SE, pupae/female/48h) of *Encarsia formosa* Gahan, 1924 (Hymenoptera: Aphelinidae) females from local populations Bujanovac (B), Mršinci (M), Negotin (N), Pirot (P), Svilajnac (S) and Zemun (Z), and the Dutch strain (D).

Population	Oviposition (days)									
	1-2	3-4	5-6	7-8	9-10	11-12	13-14	15-16	17-18	19-20
B	21.73 ab* (± 1.54)	28.85 a (± 1.70)	25.00 ab (± 1.57)	25.61 a (± 1.78)	21.79 ab (± 1.31)	19.47 a (± 1.54)	20.73 a (± 1.04)	16.77 ab (± 1.35)	13.50 a (± 1.00)	6.00 a (± 3.56)
D	22.40 a (± 1.57)	28.07 a (± 0.74)	27.10 a (± 1.52)	26.48 a (± 1.70)	23.32 a (± 1.12)	18.03 a (± 1.24)	16.85 a (± 1.15)	15.50 abc (± 0.32)	5.50 a (± 3.20)	-
M	17.68 c (± 0.87)	20.38 c (± 0.83)	18.12 d (± 0.92)	19.39 bc (± 2.04)	15.76 c (± 0.81)	18.07 a (± 2.20)	15.98 a (± 0.81)	6.25 c (± 3.62)	-	-
N	20.32 abc (± 0.73)	23.77 b (± 1.02)	21.85 bcd (± 1.40)	19.19 bc (± 0.87)	18.77 bc (± 1.06)	16.38 a (± 0.80)	7.50 b (± 4.35)	-	-	-
P	17.65 c (± 0.62)	23.78 b (± 1.23)	20.00 cd (± 1.37)	18.00 c (± 1.20)	17.34 c (± 1.80)	16.51 a (± 0.48)	15.88 a (± 1.03)	18.92 a (± 4.60)	6.50 a (± 3.77)	-
S	20.65 abc (± 1.00)	24.78 b (± 1.66)	23.31 abc (± 1.84)	20.10 bc (± 0.87)	18.50 bc (± 0.80)	17.78 a (± 1.02)	17.01 a (± 0.71)	11.79 abc (± 3.91)	8.83 a (± 3.56)	5.50 a (± 3.06)
Z	18.73 bc (± 0.57)	26.22 ab (± 1.10)	24.52 ab (± 1.95)	22.28 ab (± 1.03)	18.71 bc (± 1.33)	16.80 a (± 1.26)	11.42 ab (± 2.86)	7.75 bc (± 4.52)	-	-

* The mean values with different letters in the same column are significantly different (ANOVA followed by Fisher LSD's test, $p < 0.05$)

Table 3. Total parasitism (means \pm SE, pupae/female/lifetime) and adult emergence (means \pm SE, adults/female) of *Encarsia formosa* Gahan, 1924 (Hymenoptera: Aphelinidae) females from local populations Bujanovac (B), Mršinci (M), Negotin (N), Pirot (P), Svilajnac (S) and Zemun (Z), and the Dutch strain (D).

Population	Total parasitism	Adult emergence
B	199.53 \pm 3.22 a*	171.18 \pm 3.57 a
D	183.25 \pm 2.73 ab	159.58 \pm 2.26 ab
M	131.64 \pm 6.97 ef	116.41 \pm 6.91 e
N	127.76 \pm 5.33 f	112.90 \pm 4.30 e
P	154.57 \pm 7.04 cd	133.09 \pm 7.87 cd
S	168.25 \pm 10.58 bc	146.29 \pm 8.02 bc
Z	146.32 \pm 4.94 de	128.15 \pm 3.34 de

* The mean values with different letters in the same column are significantly different (ANOVA followed by Fisher LSD's test $p < 0.05$).

Table 4 shows the instantaneous rates of increase of *E. formosa* populations starting from the 16-day oviposition interval (the choice was based on the fact that massive emergence of adults from eggs laid on the first day occurred after 14 days), until the end of oviposition. Statistically significant differences were detected among populations after 16 days ($F_{6,21} = 12.68$, $p < 0.001$), 18 days ($F_{6,21} = 11.89$, $p < 0.001$) and 20 days ($F_{6,21} = 24.52$, $p < 0.001$). At the end of oviposition, the highest r_i values were found in populations B (0.240 day⁻¹) and D (0.239 day⁻¹), significantly higher than in all other populations. The lowest r_i , found in population N (0.212 day⁻¹), was 1.12 times lower than the top values.

Table 4. The instantaneous rate of increase (means \pm SE, day⁻¹) of *E. formosa* females from local populations Bujanovac (B), Mršinci (M), Negotin (N), Pirot (P), Svilajnac (S) and Zemun (Z), and the Dutch strain (D).

Population	Oviposition (days)		
	16	18	20
B	0.303 \pm 0.001 a*	0.267 \pm 0.001 a	0.240 \pm 0.001 a
D	0.302 \pm 0.001 ab	0.267 \pm 0.001 a	0.239 \pm 0.001 a
M	0.276 \pm 0.004 de	0.244 \pm 0.003 d	0.218 \pm 0.003 c
N	0.268 \pm 0.002 e	0.237 \pm 0.002 d	0.212 \pm 0.002 d
P	0.279 \pm 0.003 de	0.245 \pm 0.004 cd	0.220 \pm 0.003 c
S	0.287 \pm 0.003 cd	0.255 \pm 0.003 bc	
Z	0.292 \pm 0.007 bc	0.258 \pm 0.007 ab	

* The mean values with different letters in the same column are significantly different (ANOVA followed by Fisher LSD test, $p < 0.05$).

4. Discussion

Similar data on the development time of *E. formosa* on *T. vaporariorum* as a host have been reported from other studies. Arakawa (1982) had found the Dutch strain to develop for 15 days on tobacco plants at the temperature of 25 °C. The development of the Dutch strain of *E. formosa* from eggs to adults on whiteflies has also been reported to last from 11.9 to 15 days at 27 °C on tomato (Burnett 1949, Stenseth 1971) and bean plants (Madueke & Coaker 1984, Donnell & Hunter 2002). Dutch strain juveniles had needed 14 days to develop on pepper, aubergine and cucumber at 22.5–25 °C (Woets & van Lenteren 1976). Studying a local population in Serbia reared on beans, Perić (1999) had found that juveniles required 14.8 days to complete development at 27 °C. The development of juveniles of the Beltsville strain of *E. formosa* had lasted 14.42 days at 26 °C (Hu et al. 2002). Grille et al. (2012) had reported a preimaginal development time of 16.6 days (an Uruguayan parasitoid strain) when its whitefly host was parasitized at instar four on tobacco plants.

Comparing data from other studies on adult longevity of *E. formosa* in the presence or absence of hosts, Vet & van Lenteren (1981) and van Lenteren et al. (1987) inferred that being given access to hosts shortened the longevity of *E. formosa*. The parasitoid females are known to resorb their follicles in the absence of suitable hosts, and this ovisorption may account for the extended longevity observed in the absence of hosts.

Feeding parasitoids on honey alone, Qui et al. (2004) found that the average longevity of *E. formosa* Dutch strain reared on whiteflies (at 25 °C on tobacco plants) was 11.2 days, significantly shorter than it was in our study (17.24 days). A Californian population of that parasitoid reared on whiteflies (at 27 °C on tobacco) lived as long as 35.2 days (Vet & van Lenteren 1981), significantly longer than local populations from Serbia.

Perić (1999) had reported that females of a local population of *E. formosa* lived 13.1 days on the average at 27 °C in the presence of whitefly larvae on beans. Such considerable differences may be attributed to different methodologies (different ways of offering hosts to parasitoid females, and different host plants). Wasp females of an Iranian population had lived the average 27.73 days at 25 °C in the presence of *T. vaporariorum* hosts on tobacco (Gholamzadeh et al. 2012). In our present experiment, the females of population D, in host presence, lived 11.2 days on the average. Madueke (1979) had reported a similar longevity of *E. formosa* Dutch strain of 11.4 days (at 27 °C on beans) in the presence of whitefly larvae. On the other hand, Jansen (1974) had reported a higher female longevity of that commercial strain after parasitizing *T. vaporariorum* nymphs, i.e. 15.6 days (at 27 °C on tomato), while Stouthamer and Mak (2002) found it to be even higher, 17.7 days (at 25 °C on tobacco). Longevities of 15.7 days (at 24 °C) and 8.15 days (at 27 °C) had also been reported by Burnett (1949) for the Dutch strain of *E. formosa* with *T. vaporariorum* on tomato available throughout the parasitoid life.

Encarsia species have low parasitism rates at emergence, which increase gradually to their maximum level, maintained for some time, and then decreases during the last phase of adult life (Qiu et al. 2004).

Studying local population in Serbia, at 27 °C, Perić (1999) had found similar values of total parasitism, around 200 pupae/female, and 42% of the total number of parasitized pupae were parasitized in the first five days. Parasitism of population D females in our experiment was similar to the values reported from other studies in which the Dutch strain had been examined on greenhouse whitefly as the host. Madueke (1979) had recorded a total parasitism of 160.2 pupae/female during the first 20 days of female life at 22.5 °C on bean plants. Bethke et al. (1991) had reported an average parasitism rate (at 25.4 °C on tobacco) of 18.2 pupae/female/48h, while it was 18.25 pupae/female/48h in our experiment (when total parasitism was divided by the number of 48h intervals). On the other hand, Stouthamer & Mak (2002) had found females of the Dutch strain to have parasitized 33.7 pupae/female in the first two days of oviposition and 44.1 pupae/female (at 25 °C, on tobacco) over the following two days, which is significantly more than it was recorded in our experiment.

Significant differences in adult emergence resulted mostly from the total parasitism of populations because the proportion of total emerged adults was similar, ranging from 86% to 88%. On the other hand, oviposition duration may affect total parasitism, and consequently the adult emergence too.

Population growth rate is a more reliable indicator of a population's ability to exploit its environment by increasing in number, compared to individual life history traits. Construction of life tables and calculation of intrinsic rates of increase and some other demographic parameters has been widely used for studying the effects of different factors on arthropod population growth. The approach has been used in several studies of *Encarsia* species parasitizing whitefly hosts (Enkegaard 1993, Gould et al. 1995, Gholamzadeh et al. 2012). The instantaneous rate of increase is an alternative measure of population growth that integrates both survivorship and reproduction, yet it is not as time- and labor-consuming as life table bioassays (Walthall & Stark 1997).

The data acquired in the present study show that females of the local *E. formosa* population Bujanovac (B) showed the most promising results for integrated control of whitefly in Serbia, with regard to their longevity and reproductive potential, when compared to the Dutch strain: there were no significant differences in life history traits except longevity in host presence, which was significantly shorter in the latter. Comparing to commercial population D, local populations S was not statistically different in longevity, survival, total parasitism and adult's emergence, but developed statistically significantly longer and achieved a significantly lower rate of population growth. In relation to the population B, population S showed significantly less favorable of all the study parameters (except longevity).

The results provide a starting point for further evaluation of local populations of this parasitoid wasp as a biological agent used for controlling *T. vaporariorum* in Serbia. Further research should also incorporate genetic backgrounds and greenhouse experiments with local populations, as well as an evaluation of insecticides in laboratory bioassays and greenhouse trials, focusing particularly on population-level endpoints.

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References

- Arakawa, R. (1982): Reproductive Capacity and Amount of Host-feeding of *Encarsia formosa* Gahan (Hymenoptera, Aphelinidae). – *Journal of Applied Entomology* **93**: 175–182.
- Bethke, J.A., Nuessly, G.S., Paine, T.D. & Redak, R.A. (1991): Effect of Insect-Host Plant Associations on Selected Fitness components of *Encarsia formosa* (Gahan) (Hymenoptera: Aphelinidae). – *Biological Control* **1**: 164–169.
- Brødsgaard, H.F. & Albajes, R. (1999): Insect and mite pests. – In: Albajes, R., Lodovica Gullino, M., Van Lenteren, J.C. & Elad, Y. (eds.): *Integrated Pest and Disease Management in Greenhouse Crops*. – Kluwer Academic Publishers, 48–60, Nederland.
- Burnett, T. (1949): The Effect of Temperature on an Insect-Parasite Population. – *Ecology* **30**: 113–134.
- CABI (1993): *Trialeurodes vaporariorum*. – *Invasive Species Compendium*, Wallingford, UK, CAB International, available online: <http://www.cabi.org/isc>.
- Donnell, D.M. & Hunter, M.S. (2002): Developmental Rates of Two Congeneric Parasitoids, *Encarsia formosa* and *E. pergandiella* (Hymenoptera: Aphelinidae), Utilizing Different Egg Provisioning Strategies. – *Journal of Insect Physiology* **48**: 487–493.
- Enkegaard, A. (1993): *Encarsia formosa* Parazitizing the Poinsettia-strain of the Cotton Whitefly, *Bemisia tabaci*, on Poinsettia: Bionomics in Relation to Temperature. – *Entomologia Experimentalis et Applicata* **69**: 251–261.
- Gentz, M.C., Murdoch, G. & King, G.F. (2010): Tandem use of selective insecticides and natural enemies for effective, reduced-risk pest management. – *Biocontrol* **52**: 208–215.
- Gerling, D. (1990): Whiteflies: Their Bionomics, Pest Status and Management. – Intercept Limited, Andover, UK.
- Gholamzadeh, M., Ghadamyari, M., Salehi, L. & Hoseininaveh, V. (2012): Effects of Amitraz, Buprofezin and Propargite on Some Fitness Parameters of the Parasitoid *Encarsia formosa* (Hym.: Aphelinidae), Using Life Table and IOBC Methods. – *Iranian Journal of Agricultural Research* **31**: 1–14.
- Grille, G., Lorenzo, M.E., Burla, J.P., Franco, J. & Basso, C. (2012): Parasitoid Niches of *Encarsia formosa* and *Encarsia lycopersici* (Hymenoptera: Aphelinidae) Exploiting *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae). – *Florida Entomologist* **95**: 1024–1030.
- Gorman, K., Hewitt, F., Denholm, I. & Devine, G.J. (2001): New Developments in Insecticide Resistance in the Glasshouse Whitefly (*Trialeurodes vaporariorum*) and the Two-Spotted Spider Mite (*Tetranychus urticae*) in the UK. – *Pest Management Science* **58**: 123–130.
- Gorman, K., Devine, G., Bennison, J., Coussons, P., Punchard, N. & Denholm, I. (2007): Rapid Report of Resistance to the Neonicotinoid Insecticide Imidacloprid in *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae). – *Pest Management Science* **63**: 555–558.
- Gould, J.R., Bellows, T.S. & Paine, T.R. (1995): Preimaginal Development, Adult Longevity and Fecundity of *Encarsia inaron* (Hym.: Aphelinidae) Parasitizing *Siphoninus phillyreae* (Hom.: Aleyrodidae) in California. – *Entomophaga* **40**: 55–68.
- Henter, H. & van Lenteren, J.C. (1996): Variation Between Laboratory Populations in the Performance of the Parasitoid *Encarsia formosa* on Two Host Species, *Bemisia tabaci* and *Trialeurodes vaporariorum*. – *Entomologia Experimentalis et Applicata* **80**: 427–434.

- Hoddle, M.S., van Driesche, R.G. & Sanderson, J.P. (1998): Biology and Use of the Whitefly Parasitoid *Encarsia formosa*. – Annual Review of Entomology **43**: 645–649.
- Hu, J.S., Gelman, D.B. & Blackburn, M.B. (2002): Growth and Development of *Encarsia formosa* (Hymenoptera: Aphelinidae) in the Greenhouse Whitefly, *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae): Effect of Host Age. – Archives of Insect Biochemistry and Physiology **49**: 125–136.
- Jansen, W.T. (1974): Enkele Aspecten van de Oecologie *Trialeurodes vaporariorum* Westwood en Zijn Parasiet *Encarsia formosa* Gahan. – Ph.D. thesis, University of Leiden.
- Kajita, H. & van Lenteren, J.C. (1982): The Parasite-Host Relationship Between *Encarsia formosa* (Hymenoptera, Aphelinidae) and *Trialeurodes vaporariorum* (Homoptera, Aleyrodidae). XIII. Effect of Low Temperatures on Egg Maturation of *Encarsia formosa*. – Journal of Applied Entomology **93**: 430–439.
- Karatolos, N., Denholm, I., Williamson, M., Nauen, R. & Gorman, K. (2010): Incidence and Characterisation of Resistance to Neonicotinoid Insecticides and Pymetrozine in the Greenhouse Whitefly, *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae). – Pest Management Science **66**: 1304–1307.
- Němec, V. & Starý, P. (1984): Population Diversity of *Encarsia formosa*, a Biocontrol Agent in Glasshouses. – Entomologia Generalis **9**: 231–236.
- Madueke, E.D.N. (1979): Biological Control of *Trialeurodes vaporariorum*. – PhD thesis, University of Cambridge.
- Madueke, E.D.N. & Coaker, J.H. (1984): Temperature Requirements of the Whitefly *Trialeurodes vaporariorum* (Homoptera: Aleyrodidae) and its Parasitoid *Encarsia formosa* (Hymenoptera: Aphelinidae). – Entomologia Generalis **9**: 149–154.
- Martin, J.H., Mifsud, D. & Rapisarda, C. (2000): The Whiteflies (Hemiptera: Aleyrodidae) of Europe and Mediterranean Basin. – Bulletin of Entomological Research **90**: 407–448.
- Palevsky, E., Sorokey, V., Weintraub, P., Mansour, F., Abu-Moach, F. & Gerson, U. (2001): How specific is the Phoretic Relationship Between Broad Mite, *Polyphagotarsonemus latus* (Banks) (Acari: Tarsonemidae), and its Insect Vectors? – Experimental and Applied Acarology **25**: 217–224.
- Perić, P. (1999): Use of Autochthonous Species of Parasitoids from the Genus *Encarsia* for the Biological Control of Whitefly (*Trialeurodes vaporariorum* Westwood) in glasshouses. – Ph.D thesis, Faculty of agriculture, University of Novi Sad (in Serbian).
- Petanović, R., Marčić, D. & Vidović, B. (2010): Mite pests in Plant Crops—Current issues, Inovative Approaches and Possibilities for Controlling Them. – Pesticides and Phytomedicine **25**: 9–27 (in Serbian).
- Pilkington, L.J., Messelink, G., van Lenteren, Y.C. & Le Mottee, K. (2010): “Protected Biological Control”—Biological Pest Management in the Greenhouse Industry. – Biological Control **52**: 216–220.
- Prijović, M., Drobnjaković, T., Marčić, D., Perić, P. & Stamenković, S. (2012): Efficacy of Insecticides of Natural Origin in Whitefly (*Trialeurodes vaporariorum*) Control on Tomato. – Acta Horticulturae **960**: 359–364.
- Prijović, M., Škaljac, M., Drobnjaković, T., Žanić, K., Perić, P., Marčić, D. & Puizina, J. (2014): Genetic variation of the greenhouse whitefly, *Trialeurodes vaporariorum* (Hemiptera: Aleyrodidae), among populations from Serbia and neighbouring countries, as inferred from COI sequence variability. – Bulletin of Entomological Research **104**: 357–366.
- Polaszek, A., Evans, G.A. & Bernett E.D. (1992): *Encarsia* Parasitoids of *Bemisia tabaci* (Hymenoptera: Aphelinidae, Homoptera: Aleyrodidae): a Preliminary Guide to Identification. – Bulletin of Entomological Research **82**: 375–392.
- Qiu, Y.T., van Lenteren, Y.C., Drost, C.J. & Doodeman, A.M. (2004): Life History Parameters of *Encarsia formosa*, *Eretmocerus eremicus* and *E. mundus*, Aphelinid Parasitoids of *Bemisia argentifolii* (Homoptera: Aleyrodidae). – European Journal of Entomology **101**: 83–94.
- Speyer, E.R. (1927): An Important Parasite of the Greenhouse Whitefly (*Trialeurodes vaporariorum* Westwood). – Bulletin of Entomological Research **17**: 301–308.

- Stenseth, C. (1971): Temperaturens Effekt på Utvikling hos Veksthusmellus (*Trialeurodes vaporariorum* Westwood). – *Forsk Forsøk Landbruk* **22**: 493–496.
- Stenseth, C. (1977): The time of Development of *Trialeurodes vaporariorum* and *Encarsia formosa* at Constant and Alternating Temperatures, and its Importance for the Control of *Trialeurodes vaporariorum*. – In: Smith, F.F. & Webb, R.E. (eds.): *Pest Management in Protected Culture Crops* **85**: 65–69.
- Stouthamer, R. & Mak, F. (2002): Influence of Antibiotics on the Offspring Production of the Wolbachia-Infected Parthenogenetic Parasitoid *Encarsia formosa*. – *Journal of Invertebrate Pathology* **80**: 41–45.
- Szabo, E.E., Van Lenteren, J.C. & Huisman, P.W.T. (1993): Development time, Survival and Fecundity of *Encarsia formosa* on *Bemisia tabaci* and *Trialeurodes vaporariorum*. – *Bulletin IOBC/WPRS* **16**: 173–176.
- Van Lenteren, J.C. & Woets, J. (1988): Biological and Integrated Control in Greenhouses. – *Annual Review of Entomology* **33**: 239–269.
- Van Lenteren, J.C., Roskam, M.M. & Timmer, R. (1997): Commercial Mass Production and Pricing of Organisms for Biological Control of Pests in Europe. – *Biological Control* **19**: 143–149.
- Van Lenteren, J.C. & Martin, G. (1999): Biological control of whiteflies. – In: Albajes, R., Lodovica Gullino, M., van Lenteren, J.C. & Elad, Y. (eds.): *Integrated Pest and Disease Management in Greenhouse Crops*. – Kluwer Academic Publishers/Nederland, 202–215.
- Vargas, R.I., Ramadan, M., Hussain, T., Mochizuki, N., Bautista, R.C. & Stark, J.D. (2002): Comparative demography of six fruit fly (Diptera: Tephritidae) parasitoids (Hymenoptera: Braconidae). – *Biological Control* **25**: 30–40.
- Vet, L.E.M. & Van Lenteren, J.C. (1981): The Parasite-Host Relationship Between *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) and *Trialeurodes vaporariorum* (Westwood) (Homoptera: Aleyrodidae). X. A Comparison of Three *Encarsia* spp. and one *Eretmocerus* sp. to Estimate Their Potentialities in Controlling Whitefly on Tomatoes in Greenhouse with a Low Temperature Regime. – *Journal of Applied Entomology* **91**: 327–348.
- Walthall, W.K. & Stark, J.D. (1997): Comparison of Two Population-Level Ecotoxicological Endpoints: the Intrinsic (rm) and Instantaneous (ri) Rates of Increase. – *Environmental Toxicology and Chemistry* **16**: 1068–1073.
- Wisler, G.C., Duffu, J.E., Liu, H.Y. & Li, R.H. (1998): Ecology and Epidemiology of Whitefly-Transmitted Closteroviruses. – *Plant Disease* **82**: 270–280.
- Whalon, M.E., Mota-Sanchez, D., Hollingworth, R.M. & Duynslager, L. (2014): Arthropod Pesticide Resistance Database. – www.pesticideresistance.com.
- Zahradnik (1963): Aleyrodina. – *Die Tierwelt Mitteleuropas* (N.S.) **4**: 1–19.
- Zchori-Fein, E., Roush, R.T. & Hunter, M.S. (1992): Male Production Induced by Antibiotic Treatment in *Encarsia formosa* (Hymenoptera: Aphelinidae), an Asexual Species. – *Experientia* **48**: 103–105.

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