

Biological parameters of the egg parasitoid *Ooencyrtus gonoceri*

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Abstract

Ooencyrtus gonoceri Viggiani (Hymenoptera Encyrtidae) is a poorly known egg parasitoid species with an apparently rare occurrence in the Mediterranean basin. It was originally identified in southern Italy emerging from *Gonocerus acuteangulatus* (Goeze) eggs and successively recorded also from Spain. Recently *O. gonoceri* emerged from sentinel egg batches of *Halyomorpha halys* (Stal) (Hemiptera Pentatomidae) in central Italy. Due to the scanty data on this species, biological and demographic parameters of *O. gonoceri* were investigated under laboratory conditions on the alternative host *Graphosoma italicum italicum* (Muller) (Hemiptera Pentatomidae). Estimated fecundity was over 200 eggs/female and the mean progeny production per female was high (173.76 specimens). At the standard rearing condition (26 °C) the development time of both sexes was similar and adults emerged after two weeks. Moreover *O. gonoceri* females lived much longer than males and the host feeding behaviour resulted irrelevant for the parasitoid longevity. The main biological parameters of *O. gonoceri* were similar to those reported for other cogenetic species. However, this species appeared to be a very effective egg parasitoid if compared with *Ooencyrtus telenomicida* (Vassiliev) reared on the same host.

Key words: *Graphosoma italicum italicum*, Heteroptera, Italy, laboratory rearing, life table, reproductive parameters.

Introduction

Encyrtidae (Hymenoptera) is one of the largest families of the Chalcidoidea (Insecta Hymenoptera), comprising nearly 3.200 described species (Noyes, 2019). Almost all species are endoparasitoids of other insects as well as spiders, mites, and ticks. The majority of species includes solitary primary parasitoids but some species are gregarious, polyembryonic, or secondary parasitoids (Noyes, 1988). *Ooencyrtus* Ashmead is a speciose, cosmopolitan genus of Encyrtidae with over 200 described species (Noyes, 2019). Several species were used as biological control agents and some other play an important role in the natural control of many insect pests in agriculture and forestry (e.g. Huang and Noyes, 1994; van Lenteren *et al.*, 2003; Zhang *et al.*, 2005; Tunca *et al.*, 2016; Liu and Mottern, 2017; Ganjisaffar and Perring, 2020).

Ooencyrtus gonoceri Viggiani was described from material collected in Sicily, southern Italy, in 1971. This parasitoid emerged from eggs of *Gonocerus acuteangulatus* (Goeze) (Hemiptera Coreidae) collected during a field survey for natural antagonists suitable for the control of this bug pest (Viggiani, 1971). *O. gonoceri* was considered rare after Genduso and Mineo (1973; 1974) and not being able to play a relevant role in the control of *G. acuteangulatus* in the field (Mineo and Lucido, 1974). More recently, the species was collected in 2004 in Spain from eggs of *G. acuteangulatus*, *Graphosoma italicum italicum sensu* Lupoli (2017), and *Graphosoma semipunctatum* (F.) (Hemiptera Pentatomidae) (Guerrieri *et al.*, 2009), and in 2017 in central Italy (Tuscany) from eggs of *Halyomorpha halys* (Stal) (Hemiptera Pentatomidae) (LM and GSP, unpublished data), during a survey for the autochthonous egg parasitoids of the invasive bug pest.

Due to scarcity of data on *O. gonoceri* (e.g. Mineo, 1973; Viggiani and Mineo, 1974), the aims of this work were to: 1) evaluate the main biological parameters of *O. gonoceri* in the laboratory condition using *Graphosoma italicum italicum* (Muller) as a host and 2) compare the main biological traits of *O. gonoceri* with those of other *Ooencyrtus* species, in particular *Ooencyrtus telenomicida* (Vassiliev) reared on the same host and at the same laboratory conditions.

Materials and methods

Insect rearing

O. gonoceri adults (n = 16 adults) were obtained in July 2017 from parasitized *H. halys* sentinel egg batches (n = 2). The fresh eggs batches (n = 32, 896 eggs) were placed in a pear orchard in Coltano (Pisa, Tuscany) in the attempt to find egg parasitoids suitable for the control of this invasive species. Identity of the specimens was confirmed by comparing them with the type series of *O. gonoceri* deposited at the Laboratorio Ermenegildo Tremblay of Università di Napoli Federico II (Portici, Italy) (see result section for details).

The parasitoid colony was established in the laboratory using egg batches from the alternative host *G. italicum italicum*. As already reported in Mineo (1973), Binazzi *et al.* (2015) and Roversi *et al.* (2018), *G. italicum italicum* is a suitable host for rearing different species of *Ooencyrtus*. Besides, in our study, *G. italicum italicum* was selected to compare the biological traits of *O. gonoceri* with those of *O. telenomicida* using the same natural host and rearing condition (Roversi *et al.*, 2018).

G. italicum italicum is easy to rear under laboratory

conditions as it is less prone to inbreeding, cannibalism and population decline due to overcrowding. Moreover, it was selected as an alternate host for the parasitoids due to high-rate egg production even in a medium-size rearing facility (Binazzi *et al.*, 2015; Roversi *et al.*, 2018). The first colonies were established at the beginning of September 2012 by collecting wild adults and nymphs (1st to 5th instar) in the field. Thereafter, adults were transferred into insect cages and reared following the methods described by Binazzi *et al.* (2015). Females laid batches consisting of 14 eggs on average, and they were collected daily for the experiments and rearing. Rearing conditions were as follows: 28 ± 1 °C, $60 \pm 10\%$ RH, and L16:D8.

The parasitoids were reared in glass tubes (15 cm long and 2 cm diameter, closed at both ends by a plastic net of 250 μ m mesh) and fed with pure honey drops *ad libitum* replenished three times per week (Sabbatini Peverieri *et al.*, 2012; Binazzi *et al.*, 2013; Roversi *et al.*, 2018). Rearing conditions were as follows: 26 ± 1 °C, $70 \pm 5\%$ RH, L16:D8. Experiments were performed using a homogeneous cohort of parasitoids after 10 generations of laboratory rearing in the same standard conditions, and all tests were conducted from February to November 2018.

Egg stalks as a measure of *O. gonoceri* parasitization

Ooencyrtus species usually lay stalked eggs whose distal portion protrudes from the host egg (Roversi *et al.*, 2018). The egg stalk is considered to be a reliable marker of parasitization (Viggiani, 1994; Samra *et al.*, 2016) and can be easily detected using a stereomicroscope (Lloyd, 1938; Binazzi *et al.*, 2013). A test was conducted on 15 newly emerged (0–48 hours) *O. gonoceri* mated females, with no previous oviposition experience: daily, each *O. gonoceri* specimen was offered a pair of *G. italicum italicum* egg batches so that, according to Roversi *et al.* (2018), each female had *ad libitum* number of eggs. The number of egg stalks were counted daily. Host eggs with visible egg stalks were collected from the exposed batches and dissected under a stereomicroscope to record the actual number of eggs laid by parasitoid females.

Life table and demographic parameters of *O. gonoceri*

Newly emerged females and males (<24 hours) randomly chosen from the permanent colony were paired for 48 hours in glass tubes and fed with honey *ad libitum*. Successively, 15 females of *O. gonoceri* were isolated and put into 15 separate tubes and fed with honey until their death to evaluate the biological parameters of each female (see below). To calculate the *O. gonoceri* intrinsic rate of increase (r_m), two fresh egg batches of *G. italicum italicum* (<24 hours) were offered daily for 24 hours to each female until death. Two fresh egg batches were chosen because based on the results of the preliminary tests conducted under the same rearing conditions, each *O. gonoceri* female showed maximum daily oviposition of 21 eggs per day (data not shown).

Eggs were then transferred to a climatic chamber set at 26 ± 1 °C, $70 \pm 5\%$ RH, L16:D8 and checked daily for host hatching or parasitoid emergence.

The following biological parameters were recorded to generate a life table: parental female longevity, female fecundity (number of laid eggs measured by counting egg

stalks), pre-ovipositional, ovipositional and post-ovipositional periods, progeny production (offspring), emergence rate (n. offspring/n. eggs laid by females), hatching failure (n. eggs that did not produce any offspring/n. parasitized host eggs), sex ratio, development time.

The time from oviposition to adult emergence, survival rate, daily fecundity and sex ratio of offspring were used to generate $l_x m_x$ life tables (x = age in days, l_x = age-specific survival rate, m_x = age-specific productivity), and to calculate the demographic growth parameters (Birch, 1948): intrinsic rate of increase ($r_m = \ln(\Sigma l_x m_x)/T$), finite rate of increase ($\lambda = e^{r_m}$), mean generation time ($T = (\Sigma l_x m_x)/R_0$), population doubling time (Doubling time = $(\ln 2)/r_m$), net reproductive rate ($R_0 = \Sigma l_x m_x$), gross reproductive rate ($GRR = \Sigma m_x$).

The sex of the emerged parasitoids were identified under a stereomicroscope observing two distinctive characters: last abdominal segment and shape of antennae as already described in other *Ooencyrtus* species (Viggiani and Mineo, 1974; Zhang *et al.*, 2005).

Host-feeding behaviour and the effect of different feeding regimes on the *O. gonoceri* longevity

An additional experiment was conducted to evaluate potential host-feeding behavior and the influence of different feeding regimes on *O. gonoceri* longevity. From the main breeding colony, newly emerged (<24 hours) *O. gonoceri* females were isolated in glass tubes and reared until death with four different feeding regimes: i) honey, ii) *G. italicum italicum* egg batches alone, iii) honey and egg batches and iv) the control (without honey and egg batches). Each test was replicated 15 times. Females were provided with honey and egg batches as described above and monitored daily.

Statistical analysis

The life table and demographic parameters were calculated using the program developed by Hulting *et al.* (1990) based on the Birch method (1948) and Jackknife procedure (Meyer *et al.*, 1986).

Data were first checked for normality and homogeneity of variance using Kolmogorov-Smirnov and Levene tests, respectively. If these assumptions were not met, appropriate nonparametric tests were applied.

The male and female mean development time was compared using the parametric T test of Student (t). The longevity of F1 males and females was compared using the non-parametric Mann-Whitney (U) test while the comparison of female longevity in the different feeding regimens was performed using the non-parametric Kruskal-Wallis (H) test. Post hoc pairwise comparisons were carried out using the non-parametric Mann-Whitney test (U), with P values adjusted by Bonferroni correction ($P = 0.0083$). All analyses were conducted using the statistical package SPSS 20.0.

Results

Identification of *O. gonoceri*

The material examined to confirm the identity of the species included:

Holotype ♀ Polizzi G. (=Polizzi Generosa, Palermo, Sicilia) 16.VII.71 ex uova *Gonocerus acuteangulatus* su nocciuolo, G. VIGGIANI; paratypes 3♀ 3♂ same data as holotype; non-type material several ♀♀ and ♂♂ collected in the type locality from July to September 1971.

Comparison of the material has been done at the stereomicroscope (card mounted specimens) and at the microscope (slide mounted specimens).

Egg stalks as a measure of *O. gonoceri* fertility

A total of 120 egg stalks were counted corresponding to 148 eggs at the dissection, with the following frequencies of ratio between the two (stalk/eggs): 80% 1:1, 17% 1:2, 3% 1:3.

Life table of *O. gonoceri*

Two out of 15 females examined for this study resulted infertile and were excluded from the analysis. The 13 females randomly laid eggs on both egg batches. Female average daily parasitization rate was 5.68 ± 1.49 eggs/egg batch reaching a total of 206.80 ± 9.09 parasitized eggs/female. Female oviposition started the second day after emergence (2 DAE) reaching its peak on day four (4 DAE) with 8.15 ± 3.00 parasitized eggs/female.

The mean longevity of parental females was 46.61 ± 4.62 . The mean female life cycle resulted as follows: i) pre-ovipositional period 2.07 ± 0.52 days; ii) oviposition period 38.15 ± 4.26 days; and iii) post-oviposition period 4.00 ± 2.08 days. The mean offspring/female was 173.76 ± 9.20 eggs (range 23-283), with a strongly male-biased sex ratio (average 64.80%; range 36.56-75.50%). The mean pre-imaginal development time was similar between females (15.39 ± 0.12 days) and males (15.41 ± 0.64 days) ($t = 0.30$; $p = 0.76$) as reported in Mineo (1973).

The pattern of female's survival and progeny emergence trend is shown in figure 1. Survival was total during the first 20 days and decreased quite constantly

reaching 23% at the 2nd-month check, coincident with the last progeny emerged. A very low survival rate was observed after oviposition period.

On the whole, 25.5% of the progeny emerged within the 10th day of the study, 51.5% within the 20th day and 78.7% within the 30th day.

Parental females produced female offspring only in the first two weeks of their life span (12.66 ± 1.56 days). The male and female progeny offspring emergence trend of the 13 fertilized females is shown in figure 2. In total, 2259 offspring emerged from 2682 parasitized eggs, with an emergence rate of 84%. Female offspring ($n = 496$ females) lived longer than males ($n = 827$ males) ($U = 48862.00$; $n = 1324$; $P = 0.0001$). The mean longevity of offspring was 46.59 ± 3.55 days and 28.28 ± 6.8 days recorded for the female and male, respectively.

The demographic parameters of *O. gonoceri* reared on *G. italicum italicum* eggs are summarised in table 1. The intrinsic rate of natural increase (r_m) calculated for the parasitoid was 0.168 per female per day and the daily finite rate of increase (λ) was 1.18 female offsprings/female/day with a mean generation time (T) of 23 days. The net reproductive rate (R_0) of the population was 48.37 female progeny/female; at the tested conditions, the doubling time (DT) of *O. gonoceri* population was 4.1 days.

Host-feeding behaviour and the effect of different feeding regimes on the *O. gonoceri* longevity

The four different feeding regimes significantly affected female longevity ($H = 44.591$; $df = 3$; $p = 0.0001$). No differences were found between females reared on honey (45.63 ± 2.92 days) or honey and eggs (46.61 ± 4.62 days) and the same results were observed between females reared only on eggs (3.07 ± 0.12 days) and in the absence of honey or eggs (2.4 ± 0.16 days) (table 2). Our findings suggest that honey may affect parasitoid longevity while host feeding is irrelevant for parasitoid longevity.

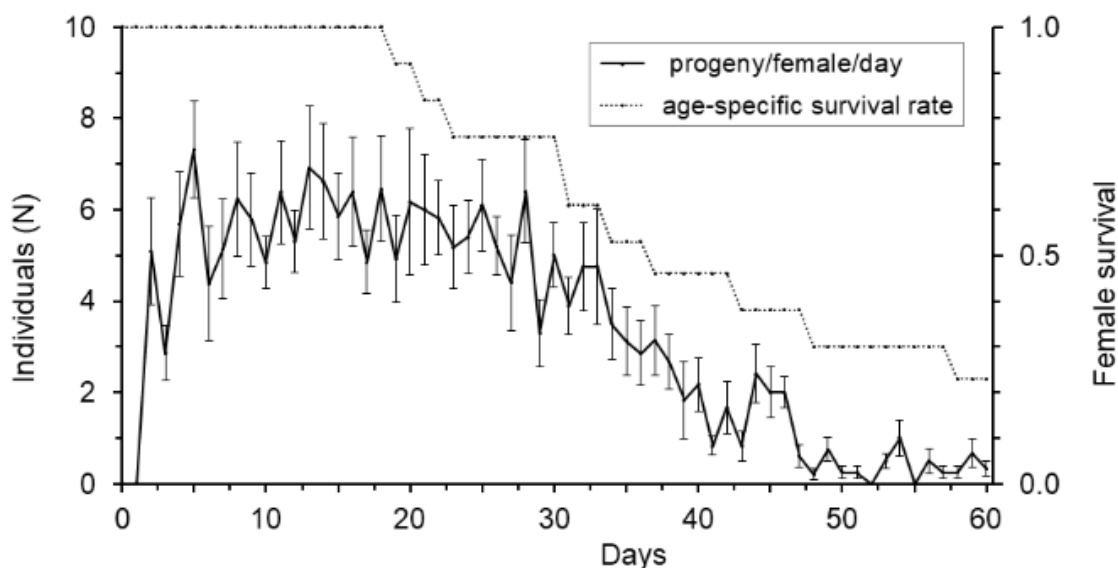


Figure 1. Mean fertility (\pm SD) and survival (%) of *O. gonoceri* females ($n = 13$) reared on *G. italicum italicum* egg batches (26 ± 1 °C, $75 \pm 5\%$ RH and L16:D8).

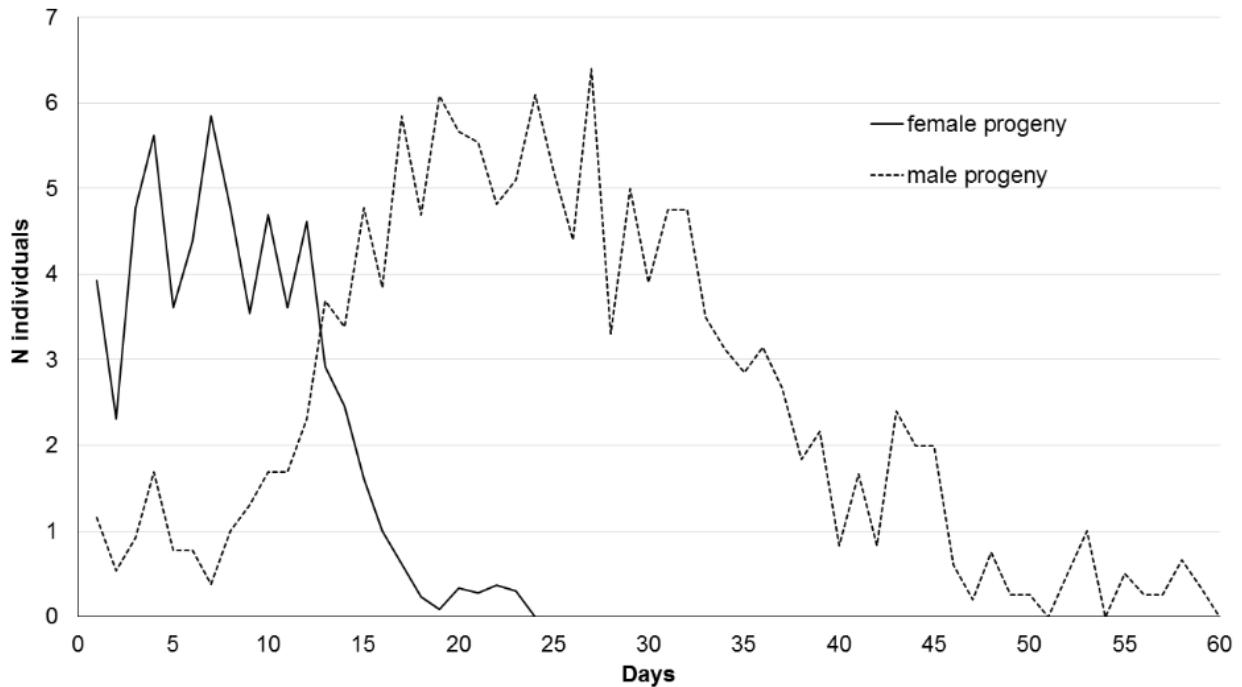


Figure 2. Female and male progeny of *O. gonoceri* females (n = 13) during their lifespan.

Table 1. Demographic parameters of *O. gonoceri* reared on *G. italicum italicum* egg batches (26 ± 1 °C, 75 ± 5% RH and L16:D8).

Parameters	Value
Intrinsic rate of increase (r_m)(day ⁻¹)	0.168 ± 0.008
Finite rate of increase (λ)	1.18
Mean generation time (T) (days)	23.02
Net reproductive rate (R_0) (female progeny/female)	48.37
Gross reproductive rate (GRR) (female progeny/female)	71.95
Doubling time (Td) (days)	4.11

Table 2. Post hoc tests among female longevities recorded in the four feeding regimens.

Post hoc	U	P
No food sources Eggs	8.733	0.818
No food sources Honey + Eggs	-32.267	0.0001
No food sources Honey	-32.503	0.0001
Eggs Honey + Eggs	-23.533	0.0001
Eggs Honey	-23.770	0.001
Honey Honey + Eggs	0.236	1.000

Discussion and conclusions

Life tables are useful to investigate insect population dynamics over time. Data on survival and mortality are pivotal to monitor population trends. Accurate biological parameters of the *O. gonoceri* egg parasitoid are reported here for the first time. This species resulted extremely prolific in the laboratory with regards to the congeneric ones, especially *O. telenomicida* (Roversi *et al.*, 2018) (*O. gonoceri*: 206.80 ± 9.09 and *O. telenomicida*: 94.57 ± 21.19 eggs/female). These important differences can be due to a longer oviposition period in *O. gonoceri* compared to *O. telenomicida* (39 vs 20 days). A positive

correlation between fecundity and the duration of the oviposition period has been already demonstrated for *Ooencyrtus anasae* Ashmead reared on *Anasa tristis* De Geer (Hemiptera Coreide) (Tracy and Nechols, 1988). *O. gonoceri* showed a higher fecundity compared to the following *Ooencyrtus* species: *O. telenomicida*, *Ooencyrtus fecundus* Ferriere et Voegelé and *Ooencyrtus pityocampae* Mercet (Samra *et al.*, 2016). This finding could be due to the different biology of the parasitoids (e.g. longer oviposition period in *O. gonoceri*) but also to the slightly different experimental set up used in these studies.

The total progeny development time showed a high synchrony between the individuals of both sexes, as

observed in *O. telenomicida* by Roversi *et al.* (2018). Moreover, male and female longevity of *O. gonoceri* was consistent with that of *O. telenomicida* reared either on the same host *G. italicum italicum* (Roversi *et al.*, 2018) or on *Stenozygum coloratum* (Klug) (Hemiptera Pentatomidae) (Samra *et al.*, 2016). The longevity of *O. gonoceri* is in line with that of other *Ooencyrtus* spp. such as *O. mevalbelus* (= *fecundus*), *O. zoeae* (= near *fecundus*), *O. pistaciae*, and *O. pityocampae* reared on the host *S. coloratum* (Samra *et al.*, 2016; 2018). Similar results were also obtained with *O. anasae* reared on *A. tristis* at comparable temperatures and rearing conditions (Tracy and Nechols, 1988). Moreover, there are no differences in longevity between parental females that laid eggs and female progeny without oviposition experience, by implying that the presence of an egg load does not affect female survival.

The emergence rate of *O. gonoceri* (84.6%) was slightly lower with respect to *O. telenomicida* (89.6%) reared on the same host, with a higher number of unhatched parasitized eggs (18% and 7%, respectively). Results were consistent with those obtained with other *Ooencyrtus* spp. such as *O. telenomicida* (85%), *O. mevalbelus* (= *fecundus*, 81.3%), *O. zoeae* (= near *fecundus*, 83.2%), *O. pityocampae* (80.7%), reared on *S. coloratum* (Samra *et al.*, 2016, 2018). Similar results (84.10%) were also observed for *O. pityocampae* reared on *Samia cynthia ricini* Boisduval (Lepidoptera Saturniidae) (Tunca *et al.*, 2016).

Female progeny is generated on average in the first 12 days of their reproductive life. A similar trend of the daily sex ratio was obtained in *O. lucidus* reared on *Bragada hilaris* (Burmeister) (Hemiptera Pentatomidae), where a higher proportion of females occurred till the day 16th and successively the male's rate increased (Ganjisaffar and Perring, 2020). The early decline of female progeny may indicate that the parental females exhaust their sperm reserve in a short time and due to the aplodiploid reproduction, typical of biparental hymenoptera parasitoids, only males were successively generated. *O. gonoceri* showed a male-biased sex ratio in contrast with Mineo (1973) that reported a female-biased sex ratio for this species. This discrepancy is probably due to the fact that in our experiment the females were isolated and could mate only once before running the bioassay. Indeed, when females and males remained paired during the experiment, female biased sex ratio is recorded, as in the case of *O. zoeae* (27.5% of males) and *O. telenomicida* reared either on *G. italicum* (28.5% of males) or on *S. coloratum* (26.1% of males). An unexpected result was the exceptionally high male ratio (approximately 60%) recorded for *O. mevalabelus* (Samra *et al.*, 2016; 2018) and *O. lucidus* (Ganjisaffar and Perring, 2020).

Temperature is one of the most important environmental factors influencing physiology and insect behaviour, including parasitoids (Ratte, 1984): lower fertility rate is observed at extreme temperatures while higher ones take place at moderate temperatures (Force and Messenger, 1964; van Lenteren *et al.*, 1987). In *Ooencyrtus nezarae* (Ishii) reared on *Riptortus clavatus* (Thunberg) (Hemiptera Alydidae) a higher fecundity was observed at 25 °C (Aung *et al.*, 2011). We suggested that *O. gonoceri* is a

species more adapted to temperate climates even though long-term consequences of constant high-temperature rearing on parasitoid fitness have been poorly investigated. As already performed for *O. telenomicida* by Roversi *et al.* (2018) this topic should be subject for further studies for this species particularly to assess the effects of global climatic change. For example, a study conducted on *O. fecundus* reared on *Aelia cognata* Fieber (Hemiptera Pentatomidae) showed that temperature played a major role in influencing the sex ratio of parasitoids (Laraichi, 1978). In particular, the development time of ooparasitoids is affected by the temperature. In the genus *Ooencyrtus*, development time generally decreases with increasing temperature reaching an *optimum* (see Power *et al.*, 2020) and this feature is pivotal for a possible mass rearing strategy in biological control programs (Roversi *et al.*, 2018).

Life table and demographic parameters calculated in the present work for *O. gonoceri* are very similar to those obtained for *O. lucidus* as for the intrinsic rates of increase of 0.168 and 0.171 d⁻¹ and the doubling time of populations, 4.11 and 4.0 d (Ganjisaffar and Perring, 2020). Reproductive parameters were also similar in both species such as fecundity (over 200 egg/females), number of offsprings, and duration of females oviposition period.

The reproductive performances of *O. gonoceri* on different hosts could generate different outputs in the studied parameters. Several native and non-native *Ooencyrtus* species display the ability to exploit *H. halys* as host, in the field, and/or in the laboratory (Roversi *et al.*, 2016; Abram *et al.*, 2017; Tunca *et al.*, 2019). However, the potential global impact of the known *Ooencyrtus* species of the parasitoid complex of *H. halys* is considered generally low compared to species belonging to other hymenopteran families, first of all scelionids or eupelmids (Abram *et al.*, 2017; Zhang *et al.*, 2017). As a consequence these parasitoids are already being used in the biological control of the brown marmorated stinkbug (*H. halys*) in Italy (MATTM, 2020).

In the experiment with different feeding regimes *O. gonoceri* female longevity was similar to that reported by Roversi *et al.* (2018) for *O. telenomicida* on the same host (*G. italicum italicum*) and it was not shortened when females were reared with only honey as a food source. As expected, carbohydrate sources had an important impact on *O. gonoceri* adult longevity compared to host feeding that was either unrecorded or irrelevant, as reported also for *O. pityocampae* (Mohammadpour *et al.*, 2018). Jervis and Kidd (1986) and Heimpel and Collier (1996) reported that the role of host feeding in adult longevity is controversial and in some species host feeding has no effect on longevity, in some it does, while yet in others it does only if a sugar source is also available. Nonetheless honey is a complex food source including not only carbohydrates.

In conclusion, *O. gonoceri* showed a long lifespan and high fertility coupled with a very short development period and an early peak for progeny production using *G. italicum italicum* as a host. Considering that knowledge on *O. gonoceri* geographical distribution and host preference is largely uncompleted, its climatic-environmental requirements should be further investigated.

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