



**HAL**  
open science

**Tendency and consequences of superparasitism for the parasitoid [i]Ooencyrtus pityocampae[/i] (Hymenoptera: Encyrtidae) in parasitizing a new laboratory host, [i]Philosamia ricini[/i] (Lepidoptera: Saturniidae)**

Hilal Tunca, Maurane Buradino, ETTY-Ambre Colombel, Elisabeth Tabone

► **To cite this version:**

Hilal Tunca, Maurane Buradino, ETTY-Ambre Colombel, Elisabeth Tabone. Tendency and consequences of superparasitism for the parasitoid [i]Ooencyrtus pityocampae[/i] (Hymenoptera: Encyrtidae) in parasitizing a new laboratory host, [i]Philosamia ricini[/i] (Lepidoptera: Saturniidae). European Journal of Entomology, 2016, 113, pp.51-59. 10.14411/eje.2016.006 . hal-01270215

**HAL Id: hal-01270215**

**<https://hal.science/hal-01270215>**

Submitted on 5 Feb 2016

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



## Tendency and consequences of superparasitism for the parasitoid *Ooencyrtus pityocampae* (Hymenoptera: Encyrtidae) in parasitizing a new laboratory host, *Philosamia ricini* (Lepidoptera: Saturniidae)

HILAL TUNCA<sup>1</sup>, MAURANE BURADINO<sup>2</sup>, ETTY-AMBRE COLOMBEL<sup>2</sup> and ELISABETH TABONE<sup>2</sup>

<sup>1</sup>Ankara University, Faculty of Agriculture, Department of Plant Protection, Diskapı, 06110 Ankara, Turkey; e-mails: htunca@ankara.edu.tr, hilaltunca@gmail.com

<sup>2</sup>INRA, UEFM Site Villa Thuret, Laboratoire BioContrôle, 90 Chemin Raymond, 06160 Antibes, France; e-mails: Maurane.Buradino@paca.inra.fr, ecolombel@sophia.inra.fr, Elisabeth.Tabone@sophia.inra.fr

**Key words.** Hymenoptera, Encyrtidae, *Ooencyrtus pityocampae*, Lepidoptera, Saturniidae, *Philosamia ricini*, self-superparasitism, host density, female age, offspring fitness

**Abstract.** The tendency for self-superparasitism and its effects on the quality of the parasitoid *Ooencyrtus pityocampae* (Mercet) (Hymenoptera: Encyrtidae) in parasitizing a new laboratory host, *Philosamia ricini* (Danovan) (Lepidoptera: Saturniidae), were investigated. In this study, female parasitoids of various ages (1-, 3- and 5-day-old) were tested individually. Parasitoids were provided with 1-day-old *P. ricini* eggs at ratios of 5, 10, 20, 30 and 40 host eggs per wasp. The tendency to superparasitize was dependent on the female's age and host density. Five-day-old females showed a strong tendency to superparasitize at low host densities. The development time of wasps in superparasitized eggs was longer than that of wasps in singly parasitized eggs. The size and longevity of adult parasitoids decreased significantly with superparasitism. This work contributes to the development of an efficient mass rearing and laboratory rearing of the parasitoid *O. pityocampae* using a new host.

### INTRODUCTION

*Ooencyrtus* is a genus of solitary polyphagous egg parasitoids, which attacks many of the insect pests of agriculture and forestry. Ten species of *Ooencyrtus* are used in biological control programs (Noyes & Hayat, 1984; Huang & Noyes, 1994). *Ooencyrtus pityocampae* (Mercet) (Hymenoptera: Encyrtidae) is the most effective parasitoid of the pine processionary moth, *Thaumetopoea pityocampa* (Denis & Schiffermüller) (Lepidoptera: Thaumetopoeidae) and is used in inundative biocontrol programs aimed at controlling this forest pest (Battisti et al., 1990; Masutti et al., 1993; Tiberi et al., 1994; Zhang et al., 2005; Binazzi et al., 2013; Samra et al., 2015).

The improvement of biocontrol programs depends on the successful mass rearing of beneficial insects. Successful mass rearing is defined as producing high quality insects at low cost (Norlund, 1998). To produce large numbers of high quality parasitoids in a laboratory or insectary, rearing methods need to be automated and environmental conditions need to be optimal, during the production process. A high quality parasitoid can be obtained by optimising their life history parameters, such as growth, development, longevity, body size, fecundity, fertility, sex ratio and generation time (Bratti & Costantini, 1991; Messing et al., 1993;

Morales Ramos et al., 1998; Gandolfi, 2002; Wajnberg et al., 2008; Consoli et al., 2010).

These parameters are very important for producing parasitoids that perform well both in a laboratory and the field. However, superparasitism can adversely affect the quality of the parasitoid. Superparasitism refers to the oviposition behaviour of parasitoid females that lay eggs in previously parasitized hosts (Gu et al., 2003; Gandon et al., 2006; Dorn & Beckage, 2007). Superparasitism can adversely affect offspring fitness as they have to compete for resources (van Alphen & Visser, 1990). Superparasitism, however, is recorded in certain situations such as (i) when two or more females search together in a patch, (ii) when unparasitized hosts are rare (egg-limited parasitoid model) and (iii) when females have many mature eggs (time limited model) (Iwasa et al., 1984; van der Hoeven & Hemerik, 1990; Visser et al., 1992; Godfray, 1994).

Superparasitism is categorized into self- and conspecific superparasitism: Self-superparasitism occurs when a female parasitoid attacks a host that has already been attacked and exploited by herself (Waage, 1986), whereas in conspecific superparasitism, a female attacks a host that has been previously attacked by a conspecific (Waage, 1986; van Dijken & Waage, 1987). Moreover, self-super-

parasitism can result in host-sharing by solitary endoparasitoids, leading eventually to the evolution of gregariousness (Riddick, 2002; Pexton & Mayhew, 2005; Khafagi & Hegazi, 2008). Many biological factors affect the incidence of superparasitism, including the biological properties of female parasitoids (e.g., age, mating status, egg load, oviposition period, density), host species, host size, host density and exposure time (Brodeur & Boivin, 2006; Shoeb & El-Heneidy, 2010). In this study, we focused on the effects of female age and host density.

Hymenopteran parasitoids are classified as either proovigenic or synovigenic (Flanders, 1950; Quicke, 1997). Proovigenic females complete oogenesis prior to emergence and lay their eggs over a relatively short period of time. In synovigenic parasitoids, however, females emerge with no or few eggs and produce eggs throughout their lifetime. Egg production and mode of parasitism are also related to female age (Jervis & Kidd, 1986; Jervis et al., 1996; Quicke, 1997). Ueno (1999) and Sirot et al. (1997) show that oviposition decisions depend upon the egg load of the female parasitoid. A higher egg load may result in parasitoids laying eggs in parasitized hosts, and in this case the probability of superparasitism increases (Keasar et al., 2006). *O. pityocampae* is also a synovigenic parasitoid and superparasitism by this species may be associated with female age.

Selection of a potential host for oviposition has a major role in determining the fitness of the parasitoid's offspring (Doutt, 1959; Vinson, 1976; Hassell, 2000). The offspring of parasitoids that oviposit in high-quality hosts (i.e. which provide sufficient food resources) are more likely to survive and be more fecund than those of parasitoids that oviposit in low-quality hosts (Bernal et al., 1999; King, 2000).

When high-quality hosts are scarce, a parasitoid may accept poor-quality hosts (Van Alphen & Vet, 1986). Hosts that are already parasitized (self or conspecific superparasitism) are generally of lower quality, as embryos developing within them have to compete for food resources (Godfray, 1994). For successful parasitism, parasitoid females must oviposit and their progeny develop in individual hosts. However, egg load, longevity of the female parasitoid and host density all affect the acceptance of both

unparasitized and parasitized hosts (Roitberg et al., 1992, 1993; Fletcher et al., 1994; Hughes et al., 1994; Sirot et al., 1997; Ueno, 1999; Islam & Copland, 2000; Hopper et al., 2013).

In this study, self-superparasitism by the solitary synovigenic parasitoid *O. pityocampae* was first tested using a new host *Philosamia ricini* (Danovan) (Lepidoptera: Saturniidae). The aim of this study was to determine whether the tendency of female parasitoids to superparasitize depended both on female age and host density. In addition, we investigated the effects of superparasitism on parasitoid progeny quality.

## MATERIAL AND METHODS

This study was conducted at the INRA-PACA Mediterranean Forest and Entomology Unit, Laboratory of Biological Control, Antibes, France. All experiments were performed under controlled conditions of  $25 \pm 1^\circ\text{C}$ , an RH of  $65\% \pm 5\%$  and a 16L:8D photoperiod.

### Study species

The *O. pityocampae* used in this study came from a stock culture established from field-collected parasitized eggs of *T. pityocampa* collected in the Bouches du Rhone province and reared on *P. ricini* eggs. Two females were isolated in glass tubes ( $7 \times 1$  cm) containing approximately 70–80 fresh *P. ricini* egg masses and a drop of bio-honey for feeding. After parasitism, the female parasitoids were removed and the tubes were maintained in an incubator ( $25 \pm 1^\circ\text{C}$ , RH  $65\% \pm 5\%$  and 16L : 8D h photoperiod). After emergence, adult female parasitoids were used for subsequent experiments and to initiate parasitoid rearing. *O. pityocampae* was reared for over 9 generations in eggs of *P. ricini*.

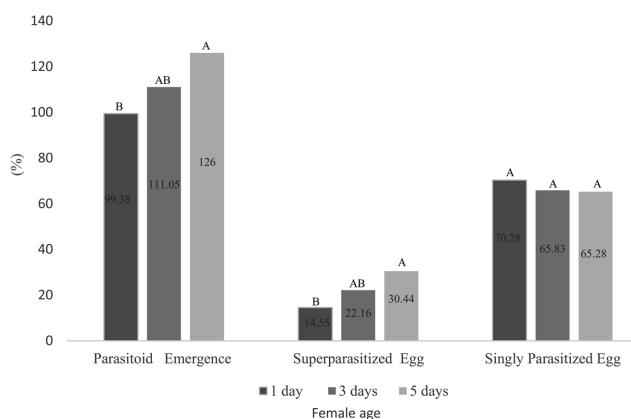
Large numbers of *P. ricini* can be easily reared on privet foliage under laboratory conditions of  $25 \pm 1^\circ\text{C}$ , RH  $65\% \pm 5\%$  and a 16L : 8D h photoperiod. *P. ricini* eggs were collected daily and kept in an incubator. Upon hatching, the neonates were placed in plastic containers ( $26 \times 12 \times 7$  cm) and fed privet foliage. Fresh foliage was provided every day, and separate containers were used for the different larval stages. At pupation, individual pupae were transferred into adult rearing cages ( $30 \times 39 \times 30$  cm). This process was repeated daily.

### Experimental procedure

To quantify the tendency to superparasitize, recently emerged females were transferred individually to glass tubes ( $1 \times 7$  cm)

**TABLE 1.** Results of the GLM analysis of the percentage emergence of parasitoids, percentage of superparasitized eggs and percentage of single-parasitized eggs.

	Source of variation	DF	SS	F	P value
Parasitoid emergence	Parasitoid age	2	0.53889	11.40	< 0.001
	Host egg number	4	0.80056	8.47	< 0.001
	Parasitoid age × Host egg number	8	0.10080	0.53	0.822
	Error	30	0.70907		
Superparasitized eggs	Parasitoid age	2	0.20936	4.10	0.027
	Host egg number	4	0.50517	4.94	0.004
	Parasitoid age × Host egg number	8	0.11046	0.54	0.817
	Error	30	0.76660		
Single parasitized eggs	Parasitoid age	2	0.02225	0.38	0.690
	Host egg number	4	0.45745	3.87	0.012
	Parasitoid age × Host egg number	8	0.03941	0.17	0.994
	Error	30	0.88680		



**Fig. 1.** Results of the percentage of parasitoid emergence, percentage of superparasitized eggs and percentage of singly-parasitized eggs on different aged females. Different letters above the bars indicate significant differences based on Duncan’s test,  $P \leq 0.05$ .

and fed bio-honey prior to experiments. These females were separated into three groups (1-, 3 and 5-day old) and were tested individually. One-day-old *P. ricini* eggs were exposed to inexperienced 1-, 3- and 5-day-old females at ratios of 5, 10, 20, 30 and 40 host eggs per wasp. At the end of the 14th day of exposure, the female parasitoid was removed and parasitized eggs were placed individually in glass tubes (7 × 1 cm). These tubes, each containing one parasitized egg, were incubated at 25 ± 1°C, RH 65% ± 5% and a 16L : 8D photoperiod until the parasitoid progeny emerged. In this study, 45 females and 315 host eggs were used. The number of individual parasitoids per host egg was evaluated by counting how many emerged from each host egg. If self-superparasitism occurs in *O. pityocampae*, it is possible to obtain two parasitoids from each *P. ricini* egg. The parasitoid emergence and frequency singly or superparasitized eggs were calculated, and percentage data on parasitoid emergence >100% exists due to superparasitism. In addition, we compared the development time, longevity and body size (weight) of the progeny that emerged from superparasitized and singly parasitized hosts.

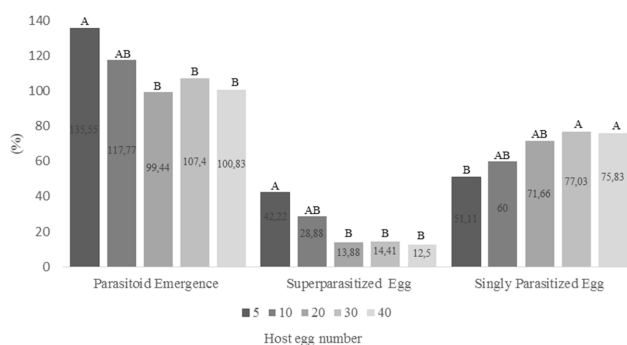
**Data analysis**

Percentage data relating to “parasitoid age” and “host egg number” was analyzed using a General Linear Model. Development time, longevity and body size (weight) were analyzed using a simple t-test (Minitab Release 14, McKenzie & Goldman, 2005; SAS Institute, 2000). Means were separated using Duncan’s test at a significant level of  $\alpha = 0.05$  (SAS Institute, 2003).

**TABLE 2.** Biological parameters of the progeny of *Ooencyrtus pityocampae* that developed in superparasitized and singly-parasitized eggs.

Biological parameters	Superparasitized eggs	Singly-parasitized eggs
Development time (day)	20.62 ± 0.10 A n = 308	19.54 ± 0.05 B n = 687
Longevity (day)	35.85 ± 0.98 B n = 42	47.76 ± 0.85 A n = 42
Body weight (mg)	0.05 ± 0.003 B n = 40	0.12 ± 0.003 A n = 40

Different letters indicate significant differences (t test,  $P < 0.05$ ).



**Fig. 2.** Results of the percentage of parasitoid emergence, percentage of superparasitized eggs, percentage of singly-parasitized eggs on different host egg numbers. Different letters above the bars indicate significant differences based on Duncan’s test,  $P \leq 0.05$ .

**RESULTS**

The statistical results are shown in Table 1. There was a significant effect of both female age and number of host eggs on parasitoid emergence and number of eggs superparasitized. Single-parasitized eggs were affected only by the number of host eggs, but there was no significant interaction between female age and number of host eggs (GLM;  $P_{\text{Emergence Rate}} = 0.822$ ,  $P_{\text{Superparasitized Egg}} = 0.817$ ,  $P_{\text{Single Parasitized Egg}} = 0.994$ ) (Table 1). The highest percentage parasitoid emergence was recorded for 5 day old parasitoids (126%) and 5 host eggs (135.55%). The highest percentage of superparasitized eggs was recorded for 3–5 day old parasitoids (22.16%–30.44%) and 5–10 host eggs (42.22%–28.88%). The highest percentage of singly parasitized egg was recorded for 1 day old parasitoids (70.28%) and 30–40 host eggs (77.03%–75.83%) (Figs 1 and 2).

In addition, there were significant differences in the development time, longevity and size of *O. pityocampae* progeny that developed in superparasitized and singly parasitized eggs ( $t_{993} = 10.33$ ,  $P < 0.000$ ;  $t_{82} = -9.15$ ,  $P < 0.000$ ;  $t_{78} = -15.65$ ,  $P < 0.000$ ) (Table 2). Development time increased and parasitoid size and longevity decreased with superparasitism. Therefore, self-superparasitism had a negative effect on these parameters of parasitoid progeny.

**DISCUSSION AND CONCLUSIONS**

*T. pityocampa* is one of the pine defoliators of high economic importance, especially in forests in the Mediterranean area. Various species of *Pinus* serve as food plants for this polyphagous forest pest (Devkota & Schmidt, 1990). Ecologically based integrated pest management strategies are very important for controlling these and other forest pests (Lieutier & Ghaïoule, 2005) This strategy is a broad-based approach that coordinates multiple tactics for ecologically and economically controlling pests of agro and forest ecosystems (Ehler, 2006). Biological control is a sustainable and environmentally friendly way of controlling insect pests.

Among the biological control approaches, augmentation of natural enemies has been suggested, and is considered safe and efficacious. In this process, natural enemies are reared in an insectary and released at target sites in large

numbers for suppression and reduction of damaging pest populations (Orr, 2009; Perera & Hemachandra, 2014). Among the parasitoids, egg parasitoids have great advantages over larval or pupal parasitoids, because egg parasitoids destroy the pest before they attack the crop. Parasitoid fitness is also very important for biological control programs. The fitness of females is mainly dependent on their ability to find hosts, and evaluating their life-history entails examining traits such as the percentage of eggs parasitized and percentage parasitoid emergence, development time, sex ratio and longevity (Bigler et al., 1991; Fournet et al., 2001; Perera & Hemachandra, 2014).

The solitary synovigenic egg parasitoid *Ooencyrtus pityocampae* can be utilized in the biological control of the pine processionary moth due to its biological characteristics, which are as follows: it is successful in parasitizing this host both in the laboratory and the field, has a short development time, long adult longevity, is able to successfully overwinter as a diapausing female and can locate its host by responding to its sex pheromone (Biliotti, 1958; Battisti et al., 1990; Tiberi, 1990; Tsankov et al., 1996, 1999; Schmidt et al., 1997, 1999; Mirchev et al., 2004). For this reason, successful mass and laboratory rearing of this parasitoid is very important. However, mass or laboratory rearing can have negative effects on parasitoid performance. One of the major problems encountered in the rearing of parasitoids is superparasitism (van Lenteren & Bigler, 2010).

Superparasitism is recorded for many species of wasp. It occurs both in nature and the laboratory, and occurs when an individual host is attacked by one or several females of the same species. Especially in nature, superparasitism is mainly recorded under certain specific conditions such as when parasitoids are unable to distinguish between previously parasitized and unparasitized hosts. Superparasitism occurs when unparasitized hosts are scarce and females have a high egg load (Salt, 1934; van Alphen & Visser, 1990; Godfray, 1994; Wanjberg et al., 2008). All these situations may also occur under laboratory conditions. Self-superparasitism by solitary parasitoids requires the most rigorous conditions to be favoured by natural selection, since it inevitably results in the elimination of supernumerary larvae (Rosenheim & Hongkham, 1996). The conditions that favour self-superparasitism are: (1) when high quality hosts are rare or the risk of adult parasitoid mortality is great and (2) when parasitoids are abundant.

However, under certain conditions, the evolutionary stable strategy predicts that many species of parasitoids are able to detect hosts that have already been parasitized by conspecifics or by themselves and avoid ovipositing eggs in these host (van Dijken & Waage, 1987; van Alphen & Visser, 1990; Visser et al., 1992; Metcalf & Luckmann, 1994). The avoidance of superparasitism could work in two ways; the wasp might recognize a parasitized host or the patch it occupies. For example *Venturia canescens* (Hymenoptera: Ichneumonidae) (Hubbard et al., 1987) *Epidinocarsis lopezi* (Hymenoptera: Encyrtidae) (van Dijken et al., 1991) and *Leptopilina heterotoma* (Hymenoptera: Eucoili-

dae) (Visser, 1993) can recognize parasitized hosts. Strand (1986) reports that *Telenomus heliothidis* (Hymenoptera: Scelionidae), which attacks the eggs of *Heliothis virescens* (Lepidoptera: Noctuidae), does not superparasitize a host after the egg of the first female has hatched.

The simplest models of superparasitism in solitary wasps depend on the type of host acceptance. Females are assumed to maximize their rate of fitness gain and previously parasitized host are treated simply as hosts of low quality (Harvey et al., 1987; Janssen, 1989; van Alphen & Visser, 1990). In solitary parasitoid species, normally only one progeny per host survives. Parasitism by more than one egg laid by the same female results in sibling competition, which results in small offspring or the death of some or all of the offspring, and a long development time (Godfray, 1987; Rosenheim, 1993; Vet et al., 1994, Pottting et al., 1997; Ode & Rosenheim, 1998; Jones et al., 1999, Mackauer & Chau, 2001). Therefore, superparasitism is an important factor in parasitoid population dynamics (Salt, 1934). However, the outcome depends on host quality, which for parasitoids is associated with the following features of the host: species, shape, size, movement, sound, chemical cues (Vinson, 1976) and age (Colinet et al., 2005). Generally large and young insects are the best hosts for wasps (Da Rocha et al., 2006; Liu et al., 2011). Parasitoids prefer hosts that are the best sources of nutrients for their offspring, and hymenopteran wasps adjust their sex ratios according to host quality in a way that maximizes the benefits. Host size is an indication of quality with larger hosts providing more resources. Charnov et al. (1981) found that sex ratios vary with host size given that host size affects parasitoid size and fitness.

*P. ricini* eggs are larger than those of the other hosts (*Aelia rostrata*, *Carpocoris* sp., *Nezara viridula*, *Dolycoris baccarum*, *Rhaphigaster nebulosa*, *Eurydema ventrale* [*E. ventralis*], *E. oleracea*, *Eurygaster maura*, *Graphosoma lineatum italicum*) of *O. pityocampae* (Halperin, 1990; Tiberi et al., 1991, 1993). In this study we tested 1-day-old *P. ricini* eggs and our results indicate that two egg (*O. pityocampae*) can successfully complete development and emerge from one host egg (*P. ricini*). Thus the nutritional resources in an egg of *P. ricini* is sufficient to support self-superparasitism by *O. pityocampae*. More parasitoid progeny can emerge from a large than a small host egg (Andrade et al., 2011). Mackauer et al. (1997) note that parasitoid growth and development varies with the amount and type of host resources available. For the parasitoid *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae), the large host *Anastrepha fraterculus* (Diptera: Tephritidae) contains more resources which support the development of larger and more competitive parasitoids with a greater reproductive potential (Chau & Mackauer, 2001). According to López et al. (2009), *D. longicaudata* more frequently superparasitizes when reared in large hosts. Mayhew & van Alphen (1999) report that the solitary parasitoid *Aphaereta genevensis* (Hymenoptera: Braconidae) normally lays one egg per host, but two or more offspring can successfully complete their development when superparasitism occurs.

On the other hand, Vinson (1984), van Alphen & Visser (1990) and Godfray (1994) report that, the survival of only one egg can be adversely affected by the host's immune response. The presence of two or more eggs in one host may enable a parasitoid to maximize the utilization of the host, in particular it could represent a strategy for overcoming the host's immune response and thus increase the probability of the offspring surviving. Similarly, a study on *Metaphycus flavus* (Hymenoptera: Encyrtidae) has demonstrated that laying several eggs in a single host suppresses the host's immune defences and reduces egg encapsulation (Kapranas et al., 2012). This would make self-superparasitism advantageous (Puttler, 1959, 1967; Streams, 1971; Blamberg & Luck, 1990; Quicke, 1997; Montoya et al., 2000; Keinan et al., 2012).

Synovigenic parasitoids are egg-limited and thus their fitness is very dependent on the number of additional eggs they can produce during their adult life (Jervis & Kidd 1996; Rosenheim, 1996). Synovigenic species can experience short-term egg limitation (Heimpel & Rosenheim, 1998; Rosenheim, 1999). The incidence of egg limitation in these species is even lower than in pro-ovigenic parasitoids. For this reason, synovigenic parasitoids can lay more eggs per host and are not selective when deciding whether to parasitize or superparasitize. In the synovigenic parasitoid *O. pityocampae*, the tendency to superparasitize increased with the age of the parasitoid females. The highest percentage was recorded for 5-day-old females (Fig. 1). The physiological basis of the two egg laying strategy may be in differences in the egg loads (number) of the different females depending on their age.

Physiological suppression associated with egg load of females of different ages is very important for superparasitism. Carbone & Rivera (2003) report a similar result for the synovigenic parasitoid *Anaphes nitens* (Hymenoptera: Mymaridae). The high egg loads of *Diaeretiella rapae* (Hymenoptera: Aphidiidae) could have resulted in them ovipositing repeatedly in the available hosts, as high egg-loads in parasitoids encourage superparasitism (Keasar et al., 2006; Silva-Torres et al., 2009).

In addition, the results of this study demonstrate that host density affects the incidence of superparasitism by *O. pityocampae*, for example, a low host density was associated with high superparasitism (Fig. 2). Therefore, even the parasitoid *O. pityocampae* could find sufficient hosts to parasitize, and thus superparasitism can be seen. This could be due to the large size of the eggs of *P. ricini*.

Kraft & van Nouhuys (2013) report that low percentages of superparasitism by the parasitoid *Pteromalus apum* (Hymenoptera: Pteromalidae) of its hosts *Melitaea cinxia* and *Melitaea athalia* (Lepidoptera: Nymphalidae) are recorded in high-host density treatments.

Similarly, Lester & Holtzer (2002) report that superparasitism by *Diaeretiella rapae* (Hymenoptera: Aphidiidae) occurs more frequently at low host densities. Hanan et al. (2015) report that, with increase in host density from 20 to 140, the percentage superparasitism by *Eretmocerus warrae* (Hymenoptera: Aphelinidae) decreases significantly.

Our experiments indicate that superparasitism by *O. pityocampae* negatively affects the development of their offspring, because it results in an increase in their development time and the production of small short lived adults. Wylie (1965) reports that, superparasitism affects the size of the parasitoid *Nasonia vitripennis* (Hymenoptera: Pteromalidae). Santolamazza Carbone & Cordero Rivera (2003) and González et al. (2006) report that superparasitism decreases the percentage emergence of the parasitoids *Dia-chasmimorpha longicaudata* (Hymenoptera: Braconidae) and *Anaphes nitens* (Hymenoptera: Mymaridae), respectively. Keasar et al. (2006) report that, superparasitism also reduces the quality of emerging parasitoids, which are small and short lived. Superparasitism increases the development time of *Venturia canescens* (Hymenoptera: Ichneumonidae) reared from third (L3) and fifth (L5) instar *Plodia interpunctella* (Lepidoptera: Pyralidae). The size of *V. canescens* emerging from L3 hosts was unaffected by superparasitism, but parasitoids from superparasitized L5 were significantly smaller than those from singly parasitized hosts (Harvey et al., 1993). Tunca & Kılınçer (2009) report that the percentage emergence and size of *Chelonus oculator* (Hymenoptera: Braconidae) decreases with increase in parasitism, but development time of the parasitoid increases with increase in superparasitism. These experimental results are supported by many previous studies (e.g., Simmonds, 1943; Gerling, 1972; Vinson & Sroka, 1978; Wylie, 1983; Eller et al., 1990; Potting et al., 1997; Hegazi & Khafagi, 2005; Chau & Maeto, 2008).

This work provides clear evidence that old females of *O. pityocampae* show a strong tendency to superparasitize when host densities are low. We also recorded that the size of the host can affect their decision to superparasitize. In addition, laying more than one egg in a host could be adaptive as it enables *O. pityocampae* to prevent the induction of the defence system in large hosts. Self-superparasitism may provide extra nutrition for the surviving parasitoid larva when host density is low. This research indicates that host density could be integrated with female age, by offering more hosts to older females. Our results may provide helpful information for improving mass and laboratory rearing of *O. pityocampae*.

## REFERENCES

- ANDRADE G.S., PRATISSOLI D., DALVI L.P., DESNEUX N. & DOS SANTOS H.J.G. JR. 2011: Performance of four *Trichogramma* species (Hymenoptera: Trichogrammatidae) as biocontrol agents of *Heliothis virescens* (Lepidoptera: Noctuidae) under various temperature regimes. — *J. Pest Sci.* **84**: 313–320.
- BATTISTI A., IANNE P., MILANI N. & ZANATA M. 1990: Preliminary accounts on the rearing of *Ooencyrtus pityocampae* (Mercet) (Hym., Encyrtidae). — *J. Appl. Entomol.* **110**: 121–127.
- BERNAL J.S., LUCK R.F. & MORSE J.G. 1999: Host influences on sex ratio, longevity, and egg load of two *Metaphycus* species parasitic on soft scales: implications for insectary rearing. — *Entomol. Exp. Appl.* **92**: 191–204.
- BIGLER F., CERUTTI F. & LAING J. 1991: First draft of criteria for quality control (product control) of *Trichogramma*. In Bigler F. (ed.): *Proceedings of the 5th Workshop of the Global IOBC Working Group "Quality Control of Mass Reared Arthropods"*,

- Wageningen, The Netherlands, March 25–28, 1991. International Organization for Biological Control, Wageningen, pp. 200–201.
- BILIOTTI E. 1958: Le parasite et prédateur de *Thaumetopoea pityocampa* Schiff. — *Entomophaga* **3**: 23–24.
- BINAZZI F., BENASSAI D., PEVERIERI S.G. & ROVERSI P.F. 2013: Effects of *Leptoglossus occidentalis* Heidemann (Heteroptera: Coreidae) egg age on the indigenous parasitoid *Ooencyrtus pityocampae* Mercet (Hymenoptera: Encyrtidae). — *Redia* **96**: 79–84.
- BLAMBERG D. & LUCK F.R. 1990: Differences in rate of superparasitism between two strains of *Comperiella bifasciata* (Howard) (Hymenoptera: Encyrtidae) parasitizing California red scale (Homoptera: Diaspididae): an adaptation to circumvent encapsulation. — *Ann. Entomol. Soc. Am.* **83**: 591–597.
- BRATTI A. & COSTANTINI W. 1991: Effects of new artificial host diets on the host-parasitoid system *Galleria mellonella* L. (Lepidoptera: Galleriidae) *Archytas marmoratus* Town. (Diptera: Tachinidae). — *Redia* **74**: 445–448.
- BRODEUR J. & BOIVIN G. 2006: *Tropic and Guild Interaction in Biological Control*. Springer, Dordrecht, 249 pp.
- CARBONE S.S. & RIVERA A.C. 2003: Egg load and adaptive superparasitism in *Anaphes nitens*, an egg parasitoid of the *Eucalyptus* snout-beetle *Gonipterus scutellatus*. — *Entomol. Exp. Appl.* **106**: 127–134.
- CHARNOV E.L., LOS-DEN HARTOGH R.L., JONES W.T. & VAN DEN ASSEM J. 1981: Sex ratio evolution in a variable environment. — *Nature* **289**: 27–33.
- CHAU A. & MACKAUER M. 2001: Preference of the aphid parasitoid *Monoctonus paulensis* (Hymenoptera: Braconidae, Aphidiinae) for different aphid species: female choice and offspring survival. — *Biol. Contr.* **20**: 30–38.
- CHAU N.N.B. & MAETO K. 2008: Intraspecific larval competition in *Meteorus pulchricornis* (Hymenoptera: Braconidae), a solitary endoparasitoid of lepidopteran larvae. — *Appl. Entomol. Zool.* **43**: 159–165.
- COLINET H., SALIN C., BOIVIN G. & HANCE T.H. 2005: Host age and fitness-related traits in a koinobiont aphid parasitoid. — *Ecol. Entomol.* **30**: 473–479.
- CONSOLI F.L., PARRA J.P.R. & ZUCCHI R.A. 2010: *Egg Parasitoids in Agroecosystems with Emphasis on Trichogramma*. Springer, Dordrecht, 482 pp.
- DA ROCHA L., KOLBERG R., MENDONÇA J.R.M.S. & REDAELLI L.R. 2006: Effects of egg age of *Spartocera denticenris* (Berg) (Hemiptera: Coreidae) on parasitism by *Gryon gallardoii* (Brethes) (Hymenoptera: Scelionidae). — *Neotrop. Entomol.* **35**: 654–659.
- DEVKOTA B. & SCHMIDT G.H. 1990: Larval development of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lepidoptera, Thaumetopoeidae) from Greece as influenced by different host plants under laboratory conditions. — *J. Appl. Entomol.* **209**: 321–330.
- DORN S. & BECKAGE N. 2007: Superparasitism in gregarious hymenopteran parasitoids: ecological, behavioural and physiological perspectives. — *Physiol. Entomol.* **32**: 199–211.
- DOUTT R.L. 1959: The biology of parasitic Hymenoptera. — *Annu. Rev. Entomol.* **4**: 161–182.
- EHLER L.E. 2006: Perspective integrated pest management (IPM): Definition, historical development and implementation, and the other IPM. — *Pest Manag. Sci.* **62**: 787–789.
- ELLER F.J., HEATH R.R. & FERKOVICH S.M. 1990: Factors affecting oviposition by the parasitoid *Microplitis croceipes* (Hymenoptera: Braconidae). — *J. Econ. Entomol.* **83**: 398–404.
- FLANDERS S.E. 1950: Regulation of ovulation and egg disposal in the parasitic Hymenoptera. — *Can. Entomol.* **82**: 134–140.
- FLETCHER J.P., HUGHES J.P. & HARVEY I.F. 1994: Life expectancy and egg load affect oviposition decisions of a solitary parasitoid. — *Proc. R. Soc. Lond. (B)* **258**: 163–167.
- FOURNET S., POINSOT D., BRUNEL E., NÉNON J.P. & CORTESERO A.M. 2001: Do female coleopteran parasitoids enhance their reproductive success by selecting high-quality oviposition sites? — *J. Anim. Ecol.* **70**: 1046–1052.
- GANDOLFI M. 2002: *Parasitoids in Artificial Mass Rearing: Mechanism of Behavioral Alterations and Significance of Olfactory Learning for Quality Maintenance*. DrSc Thesis, Swiss Federal Institute of Technology, Zurich, 71 pp.
- GANDON S., RIVERO A. & VARALDI J. 2006: Superparasitism evolution: adaptation and manipulation? — *Am. Nat.* **176**: 1–22.
- GERLING D. 1972: Notes on three species of *Eretmocerus* Halde-man occurring in Israel with a description of a new species. — *Entomol. Ber.* **32**: 156–161.
- GU H., WANG Q. & DORN S. 2003: Superparasitism in *Cotesia glomerata*: response of hosts and consequences for parasitoids. — *Ecol. Entomol.* **28**: 422–431.
- GODFRAY H.C.J. 1987: The evolution of clutch size in parasitic wasps. — *Am. Nat.* **129**: 221–233.
- GODFRAY H.C.J. 1994: *Parasitoids: Behavioural and Evolutionary Ecology*. Princeton University Press, New Jersey, 473 pp.
- GONZÁLEZ P.I., MONTOYA P., PÉREZ-LACHAUD G., CANCINO J. & LIEDO P. 2006: Superparasitism in mass reared *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) a parasitoid of fruit flies (Diptera: Tephritidae). — *Biol. Contr.* **40**: 320–326.
- HALPERIN J. 1990: Natural enemies of *Thaumetopoea* spp. (Lep., Thaumetopoeidae) in Israel. — *J. Appl. Entomol.* **109**: 425–435.
- HANAN A., SHAKEEL M., XIONG ZHAO H.E., RAZZAQ A. & WANG Q. 2015: Superparasitism and host discrimination behavior of *Eretmocerus warrae* Naumann & Schmidt (Hymenoptera: Aphelinidae). — *Turk. J. Agric. For.* **39**: 1–6.
- HARVEY I., MARRIS G. & HUBBARD S. 1987: Adaptive patterns in the avoidance of superparasitism by solitary parasitic wasps. — *Colloques INRA* **48**: 137–142.
- HARVEY J.A., HARVEY I.F. & THOMPSON D.J. 1993: The effect of superparasitism on development of the solitary parasitoid wasp, *Venturia canescens* (Hymenoptera: Ichneumonidae). — *Ecol. Entomol.* **18**: 203–208.
- HASSELL M.P. 2000: *The Spatial and Temporal Dynamics of Host-Parasitoid Interactions*. Oxford University Press, New York, 200 pp.
- HEGAZI E. & KHAFAGI W. 2005: Developmental interaction between suboptimal instars of *Spodoptera littoralis* (Lepidoptera: Noctuidae) and its parasitoid *Microplitis rufiventris* (Hymenoptera: Braconidae). — *Arch. Insect Biochem. Physiol.* **60**: 172–184.
- HEIMPEL G.E. & ROSENHEIM J.A. 1998: Egg limitation in parasitoids: a review of the evidence and a case study. — *Biol. Contr.* **11**: 160–168.
- HOPPER K.R., PRAGER S.M. & HEIMPEL G.E. 2013: Is parasitoid acceptance of different host species dynamic? — *Funct. Ecol.* **27**: 1201–1211.
- HUANG D.W. & NOYES J.S. 1994: A revision of the Indo-Pacific species of *Ooencyrtus* (Hymenoptera: Encyrtidae), parasitoids of the immature stages of economically important insect species (mainly Hemiptera and Lepidoptera). — *Bull. Br. Mus. Nat. Hist. (Entomol.)* **63**: 1–136.
- HUBBARD S.F., MARRIS G., REYNOLDS A. & ROWE G.W. 1987: Adaptive patterns in the avoidance of super-parasitism. — *J. Anim. Ecol.* **56**: 387–401.

- HUGHES J.P., HARVEY I.F. & HUBBARD S.E. 1994: Host searching behavior of *Venturia canescens* (Grav.) (Hymenoptera: Ichneumonidae): interference – the effect of mature egg load and prior behavior. — *J. Insect Behav.* **7**: 433–454.
- ISLAM K.S. & COPLAND M.J.W. 2000: Influence of egg load and oviposition time interval on the host discrimination and offspring survival of *Anagyrus pseudococci* (Hymenoptera: Encyrtidae), a solitary endoparasitoid of citrus mealybug, *Planococcus citri* (Hemiptera: Pseudococcidae). — *Bull. Entomol. Res.* **90**: 69–75.
- IWASA Y., SUZUKI Y. & MATSUDA H. 1984: Theory of oviposition strategy in parasitoids. I. Effect of mortality and limited egg number. — *Theor. Popul. Biol.* **26**: 205–227.
- JANSSEN A. 1989: Optimal host selection by *Drosophila* parasitoids in the field. — *Funct. Ecol.* **3**: 469–479.
- JERVIS M.A. & KIDD N.A.C. 1986: Host-feeding strategies in hymenopteran parasitoids. — *Biol. Rev.* **61**: 395–434.
- JERVIS M. & KIDD N. 1996: *Insect Natural Enemies: Practical Approaches to their Study and Evaluation*. Chapman and Hall, New York, 491 pp.
- JERVIS M.A., KIDD N.A.C. & HEIMPEL G.E. 1996: Parasitoid adult feeding behaviour and biocontrol – a review. — *Biocontr. News Inform.* **17**: 11–22.
- JONES W.A., GREENBERG S.M. & LEGASPI B. 1999: The effect of varying *Bemisia argentifolii* and *Eretmocerus mundus* ratios on parasitism. — *Biol. Contr.* **44**: 13–28.
- KAPRANAS A., TENA A. & LUCK R.F. 2012: Dynamic virulence in a parasitoid wasp: the influence of clutch size and sequential oviposition on egg encapsulation. — *Anim. Behav.* **83**: 833–838.
- KEASAR T., SEGOLI M., BARAK R., STEINBERG S., GIRON D., STRAND M.R., BOUSKILA A. & HARARI A. 2006: Costs and consequences of superparasitism in the polyembryonic parasitoid *Copidosoma koehleri* (Hymenoptera: Encyrtidae). — *Ecol. Entomol.* **31**: 277–283.
- KEINAN Y., KISHINEVSKY M., SEGOLI M. & KEASAR T. 2012: Repeated probing of hosts: an important component of superparasitism. — *Behav. Ecol.* **23**: 1263–1268.
- KHAFAGI W.E. & HEGAZI E.M. 2008: Does superparasitism improve host suitability for parasitoid development? A case study in the *Microplitis rufiventris* – *Spodoptera littoralis* system. — *BioControl* **53**: 427–438.
- KING B.H. 2000: Sex ratio and oviposition responses to host age and the fitness consequences to mother and offspring in the parasitoid wasp *Spalangia endius*. — *Behav. Ecol. Sociobiol.* **48**: 316–320.
- KRAFT T.S. & VAN NOUHUYS S. 2013: The effect of multi-species host density on superparasitism and sex ratio in a gregarious parasitoid. — *Ecol. Entomol.* **38**: 138–146.
- LESTER P.J. & HOLTZER T.O. 2002: Patch and prey utilization behaviors by *Aphelinus albipodus* and *Diaeretiella rapae* (Hymenoptera: Aphelinidae and Aphidiidae) on Russian wheat aphid (Homoptera: Aphididae). — *Biol. Contr.* **24**: 183–191.
- LIEUTIER F. & GHAIOULE D. 2005: *Entomological Research in Mediterranean Forest Ecosystems*. INRA, Paris, 275 pp.
- LIU Z., XU B., LI L. & SUN J. 2011: Host-size mediated trade-off in a parasitoid *Sclerodermus harmandi*. — *PLoS ONE* **6**(8), e23260.
- LÓPEZ O.P., HÉNAUT Y., CANCINO J., LAMBIN M., CRUZ-LÓPEZ L. & ROJAS J.C. 2009: Is host size an indicator of quality in the mass-reared parasitoid *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae)? — *Fla Entomol.* **92**: 441–449.
- MACKAUER M. & CHAU A. 2001: Adaptive selfsuperparasitism in a solitary parasitoid wasp: the influence of clutch size on offspring size. — *Funct. Ecol.* **15**: 335–343.
- MACKAUER M., SEQUEIRA R. & OTTO M. 1997: Growth and development in parasitoid wasps: Adaptation to variable host resources. In Dettmer K., Baurand G. & Volkl W. (eds): *Vertical Food Web Interactions*. Springer, Berlin, pp. 191–203.
- MASUTTI L., BATTISTI A., MILANI N., ZANATA M. & ZANAZZO G. 1993: In vitro rearing of *Ooencyrtus pityocampae* (Hym., Encyrtidae), an egg parasitoid of *Thaumetopoea pityocampa* (Lep., Thaumetopoeidae). — *Entomophaga* **38**: 327–333.
- MAYHEW P.J. & VAN ALPHEN J.J.M. 1999: Gregarious development in alysiine parasitoids evolved through a reduction in larval aggression. — *Anim. Behav.* **58**: 131–141.
- MCKENZIE J.D. & GOLDMAN R. 2005: *The Student Guide to Mini-tab Release 14*. Pearson Education, Boston, MA.
- MESSING R.H., KLUNGNESS L.M., PURCELL M. & WRONG T.T.Y. 1993: Quality control parameters of mass reared opine parasitoids used in augmentative biological control of tephritid fruit flies. — *Biol. Contr.* **32**: 140–147.
- METCALF R.L. & LUCKMANN W.H. 1994: *Introduction to Insect Pest Management*. John Wiley & Sons, New York, 650 pp.
- MIRCHEV P., SCHMIDT G.H., TSANKOV G. & AVCI M. 2004: Egg parasitoids of *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Thaumetopoeidae) and their impact in SW Turkey. — *J. Appl. Entomol.* **128**: 533–542.
- MONTOYA P., LIEDO P., BENREY B., BARRERA J.F., CANCINO J. & ALUJA M. 2000: Functional response and superparasitism by *Diachasmimorpha longicaudata* (Hymenoptera: Braconidae), a parasitoid of fruit flies (Diptera: Tephritidae). — *Ann. Entomol. Soc. Am.* **93**: 47–54.
- MORALES RAMOS J.A., ROJAS M.G., COLEMAN R.J. & KING E.G. 1998: Potential use of in vitro-reared *Catalaccus grandis* (Hymenoptera: Pteromalidae) for biological control of the boll weevil (Coleoptera: Curculionidae). — *J. Econ. Entomol.* **91**: 101–109.
- NORLUND D.A. 1998: Capacity and quality: keys to success in the mass rearing of biological control agents. — *Nat. Enem. Insects* **20**: 169–179.
- NOYES J.S. & HAYAT M. 1984: A review of the genera of Indo-Pacific Encyrtidae (Hymenoptera: Chalcidoidea). — *Bull. Br. Mus. Nat. Hist. (Entomol.)* **48**: 131–395.
- ODE P.J. & ROSENHEIM J.A. 1998: Sex allocation and the evolutionary transition between solitary and gregarious parasitoid development. — *Am. Nat.* **152**: 757–761.
- ORR D. 2009: Biological control and integrated pest management. In Peshin R. & Dhawan A.K. (eds): *Integrated Pest Management: Innovation-Development*. Springer, Dordrecht, pp. 207–239.
- PERERA M.C.D. & HEMACHANDRA K.S. 2014: Study of longevity, fecundity and oviposition of *Trichogrammatoidea bactrae* Nagaraja (Hymenoptera: Trichogrammatidae) to facilitate mass rearing. — *Trop. Agr. Res.* **25**: 502–509.
- PEXTON J.J. & MAYHEW P.J. 2005: Clutch size adjustment, information use and the evolution of gregarious development in parasitoid wasps. — *Behav. Ecol. Sociobiol.* **58**: 99–110.
- POTTING R.P.J., SNELLEN H.M. & VET L.E.M. 1997: Fitness consequences of superparasitism and mechanism of host discrimination in the stemborer parasitoid *Cotesia flavipes*. — *Entomol. Exp. Appl.* **82**: 341–348.
- PUTTLER B. 1959: Partial immunity of *Laphygma exigua* (Hübner) to the parasite *Hyposoter exiguae* (Viereck). — *J. Econ. Entomol.* **52**: 327–329.
- PUTTLER B. 1967: Interrelationship of *Hypera postica* (Coleoptera: Curculionidae) and *Bathyplectes curculionis* (Hymenoptera: Ichneumonidae) in the Eastern United States with particular reference to encapsulation of the parasite eggs by the weevil larvae. — *Ann. Entomol. Soc. Am.* **60**: 1031–1038.



- QUICKE D.L.J. 1997: *Parasitic Wasps*. Chapman and Hall, New York, pp. 221–255.
- RIDDICK E.W. 2002: Superparasitism occasionally predisposes *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) to develop gregariously in *Spodoptera exigua* (Hubner) (Lepidoptera: Noctuidae). — *J. Entomol. Sci.* **37**: 1–9.
- ROITBERG B.D., MANGEL M., LALONDE R.G., ROITBERG C.A., VAN ALPHEN J.J.M. & VET L. 1992: Seasonal dynamic shifts in patch exploitation by parasitic wasps. — *Behav. Ecol.* **3**: 156–165.
- ROITBERG B.D., REID M. & LI C. 1993: Choosing hosts and mates: The value of learning. In Papaj D. & Lewis A.C. (eds): *Insect Learning – Ecological and Evolutionary Perspectives*. Chapman and Hall, London, pp. 174–194.
- ROSENHEIM J.A. 1993: Single-sex broods and the evolution of nonsiblicidal wasps. — *Am. Nat.* **141**: 90–104.
- ROSENHEIM J.A. 1996: An evolutionary argument for egg limitation. — *Evolution* **50**: 2089–2094.
- ROSENHEIM J.A. 1999: The relative contributions of time and eggs to cost of reproduction. — *Evolution* **53**: 376–385.
- ROSENHEIM J.A. & HONGKHAM D. 1996: Clutch size in an obligately siblicidal parasitoid wasp. — *Anim. Behav.* **51**: 841–852.
- SALT G. 1934: Experimental studies in insect parasitism. II. Superparasitism. — *Proc. R. Soc. Lond. (B)* **114**: 455–476.
- SAMRA S., GHANIM M., PROTASOV A. & MENDEL Z. 2015: Development, reproduction, host range and geographical distribution of the variegated caper bug *Stenozygum coloratum* (Hemiptera: Heteroptera: Pentatomidae). — *Eur. J. Entomol.* **112**: 362–372.
- SANTOLAMAZZA CARBONE S. & CORDERO RIVERA A. 2003: Egg load and adaptive superparasitism in *Anaphes nitens*, an egg parasitoid of the *Eucalyptus* snout-beetle *Gonipterus scutellatus*. — *Entomol. Exp. Appl.* **106**: 127–134.
- SAS INSTITUTE 2000: *SAS/STAT User's Guide, Ver. 6, 4th ed., Vol. 1*. SAS Institute, Cary, NC.
- SAS INSTITUTE 2003: *The SAS System, Ver. 9.1*. SAS Institute, Cary, NC.
- SCHMIDT G.H., MIRCHEV P. & TSANKOV G. 1997: The egg parasitoids of *Thaumetopoea pityocampa* in the Atlas mountains near Marrakech (Morocco). — *Phytoparasitica* **25**: 275–281.
- SCHMIDT G.H., TANZEN E. & BELLIN S. 1999: Structure of egg-batches of *Thaumetopoea pityocampa* (Den. and Schiff.) (Lep., Thaumetopoeidae), egg parasitoids and rate of egg parasitism on the Iberian Peninsula. — *J. Appl. Entomol.* **123**: 449–458.
- SHOEB M.A. & EL-HENEIDY A.H. 2010: Incidence of superparasitism in relation biological aspects of the egg parasitoid *Trichogramma evanescens* (Hymenoptera: Trichogrammatidae). — *Egypt. J. Biol. Pest Contr.* **20**: 61–66.
- SILVA-TORRES C.S.A., RAMOS FILHO I.T., TORRES J.B. & BARROS R. 2009: Superparasitism and host size effects in *Oomyzus sokolowskii*, a parasitoid of diamondback moth. — *Entomol. Exp. Appl.* **133**: 65–73.
- SIMMONDS F.J. 1943: The occurrence of superparasitism in *Nemeritis canescens* Grav. — *Rev. Can. Biol.* **2**: 15–58.
- SIROT E., PLOYE H. & BERNSTEIN C. 1997: State dependant superparasitism in a solitary parasitoid: egg load and survival. — *Behav. Ecol.* **8**: 226–232.
- STRAND M.R. 1986: The physiological interactions of parasitoids with their hosts and their influences on reproductive strategies. In Waage J. & Greathead D. (eds): *Insect Parasitoids*. Academic Press, London, pp. 97–136.
- STREAMS F.A. 1971: Encapsulation of insect parasites in superparasitized hosts. — *Entomol. Exp. Appl.* **14**: 484–490.
- TIBERI R. 1990: Egg parasitoids of the pine processionary caterpillar, *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep., Thaumetopoeidae) in Italy: distribution and activity in different areas. — *J. Appl. Entomol.* **110**: 14–18.
- TIBERI R., NICCOLI A., ROVERSI P.F. & SACCHETTI P. 1991: Laboratory rearing of *Ooencyrtus pityocampae* (Mercet) on eggs of *Nezara viridula* (L.) and other pentatomids. — *Redia* **74**: 467–469.
- TIBERI R., NICCOLI A. & SACCHETTI P. 1993: Allevamento di *Ooencyrtus pityocampae* (Mercet) su uova di Rinconti Pentatomidi In Covassi M. (ed.): *Atti Convegno "Piante forestali: Avversità biotiche e prospettive di controllo biologico e integrato"* – Firenze, 5 marzo 1992. Ist. Sper. Pat. Veg., Roma, pp. 78–84.
- TIBERI R., NICCOLI A. & SACCHETTI P. 1994: Parassitizzazione delle uova di *Thaumetopoea pityocampa*: Modificazioni conseguenti al potenziamento artificiale di *Ooencyrtus pityocampae*. In: *Atti XVII Congresso nazionale Italiano di Entomologia, Udine 13–18 giugno 1994*. pp. 763–766.
- TSANKOV G., SCHMIDT G.H. & MIRCHEV P. 1996: Structure and parasitism of egg-batches of a processionary moth population different from *Thaumetopoea pityocampa* (Den. & Schiff.) (Lep. Thaumetopoeidae) found in Bulgaria. — *Boll. Zool. Agrar. Bachic.* **28**: 195–207.
- TSANKOV G., DOUMA-PETRIDOU E., MIRCHEV P., GEORGIEV G. & KOUTSAFTIKIS A. 1999: Spectrum of egg parasitoids and rate of parasitism of egg batches of the pine processionary moth *Thaumetopoea pityocampa* (Den. & Schiff.) in the Northern Peloponnes/Greece. — *J. Entomol. Res. Soc.* **1**: 1–8.
- TUNCA H. & KILINÇER N. 2009: Effect of superparasitism on the development of solitary parasitoid *Chelonus oculator* Panzer (Hymenoptera: Braconidae). — *Turk. J. Agric. For.* **33**: 463–468.
- UENO T. 1999: Host-feeding and acceptance by a parasitic wasp (Hymenoptera: Ichneumonidae) as influenced by egg load and experience in a patch. — *Evol. Ecol.* **13**: 33–44.
- VAN ALPHEN J.J.M. & VISSER M.E. 1990: Superparasitism as an adaptive strategy for insect parasitoids. — *Annu. Rev. Entomol.* **35**: 59–79.
- VAN ALPHEN J.J.M. & VET L.E.M. 1986: An evolutionary approach to host finding and selection. In Waage J.K. & Greathead D. (eds): *13th Symposium of the Royal Entomological Society of London, 18–19 September 1985*. Academic Press, London, pp. 23–61.
- VAN DER HOEVEN N. & HEMERIK L. 1990: Superparasitism as an ESS: To reject or not to reject, that is the question. — *J. Theor. Biol.* **146**: 467–482.
- VAN DIJKEN M.J. & WAAGE J.K. 1987: Self and conspecific superparasitism in *Trichogramma evanescens*. — *Entomol. Exp. Appl.* **43**: 183–192.
- VAN DIJKEN M., NEUENSCHWANDER P., VAN ALPHEN J.J.M. & HAMMOND W.N.O. 1991: Sex ratios in field populations of *Epidinocarsis lopezi* an exotic parasitoid of the cassava mealybug, in Africa. — *Ecol. Entomol.* **16**: 233–240.
- VAN LENTEREN J.C. & BIGLER F. 2010: Quality control of mass reared egg parasitoids. In Consoli F.L., Parra J.R.P. & Zucchi R.A. (eds): *Egg Parasitoids in Agroecosystems with Emphasis on Trichogramma*. Springer, New York, pp. 315–340.
- VET L.E.M., DATEMA A., JANSSEN A. & SNELLEN H. 1994: Clutch size in a larval-pupal endoparasitoid: consequences for fitness. — *J. Animal. Ecol.* **63**: 807–815.
- VINSON S.B. 1976: Host selection by insect parasitoids. — *Annu. Rev. Entomol.* **21**: 109–133.
- VINSON S.B. 1984: Parasitoid-host relationships. In Cardé R.T. & Bell W.J. (eds): *Chemical Ecology of Insects*. Chapman & Hall, New York, pp. 205–233.
- VINSON S.B. & SROKA P. 1978: Effects of superparasitism by a solitary endoparasitoid on the host, parasitoid and field samplings. — *Southwest. Entomol.* **3**: 299–303.

- VISSER M.E. 1993: Adaptive self- and conspecific superparasitism in the solitary parasitoid *Leptopilina heterotoma*. — *Behav. Ecol.* **4**: 22–28.
- VISSER M.E., VAN ALPHEN J.J.M. & HEMERIK L. 1992: Adaptive superparasitism and patch time allocation in solitary parasitoids: an ESS model. — *J. Anim. Ecol.* **6**: 93–101.
- WAJNBERG E., BERNSTEIN C. & VAN ALPHEN J. 2008: *Behavioural Ecology of Insect Parasitoid: From Theoretical Approaches to Field Applications*. Blackwell, Oxford, 445 pp.
- WAAGE J.K. 1986: Family planning in parasitoids: adaptive patterns of progeny and sex allocation. In Waage J.K. & Greathead D.J. (eds): *Insect Parasitoids*. Academic Press, London, New York, pp. 63–95.
- WYLIE H.G. 1965: Effects of superparasitism on *Nasonia vitripennis* (Walk.) (Hymenoptera: Pteromalidae). — *Can. Entomol.* **97**: 326–331.
- WYLIE H.G. 1983: Delayed development of *Microctonus vittatae* (Hymenoptera: Braconidae) in superparasitized adults of *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). — *Can. Entomol.* **115**: 441–422.
- ZHANG Y.-Z., LI W. & HUANG D.-W. 2005: A taxonomic study of Chinese species of *Ooencyrtus* (Insecta: Hymenoptera: Encyrtidae). — *Zool. Stud.* **44**: 347–360.

Received July 8, 2015; revised and accepted October 23, 2015  
Published online January 8, 2016