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

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

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**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: Thaumetopoideae) 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). Supersparasitism 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., 1996; Quicke, 1997). Tunca et al. (2016) 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 ± 1°C, an RH of 65% ± 5% and a 16L:8D phasotperiod.

### 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 were collected in glass tubes (7 × 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 ± 1°C, RH 65% ± 5% and 16L:8D h photoperiod). After emergence, adult female parasitoids were used for subsequent experiments and to initiate parasitoid rearing. *O. pityocampa* 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 ± 1°C, RH 65% ± 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 × 12 × 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 × 39 × 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 × 7 cm) containing approximately 70–80 eggs of *Philosamia ricini* (Donovan) (Lepidoptera: Saturniidae). The aim of this study was to determine whether the tendency of female parasitoids to superparasitize depended on female age and host density. In addition, we investigated the effects of superparasitism on parasitoid progeny quality.

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

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>DF</th>
<th>SS</th>
<th>F</th>
<th>P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Parasitoid emergence</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parasitoid age</td>
<td>2</td>
<td>0.53889</td>
<td>11.40</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Host egg number</td>
<td>4</td>
<td>0.80056</td>
<td>8.47</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Parasitoid age × Host egg number</td>
<td>8</td>
<td>0.10080</td>
<td>0.53</td>
<td>0.822</td>
</tr>
<tr>
<td>Error</td>
<td>30</td>
<td>0.70907</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Superparasitized eggs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parasitoid age</td>
<td>2</td>
<td>0.20936</td>
<td>4.10</td>
<td>0.027</td>
</tr>
<tr>
<td>Host egg number</td>
<td>4</td>
<td>0.50517</td>
<td>4.94</td>
<td>0.004</td>
</tr>
<tr>
<td>Parasitoid age × Host egg number</td>
<td>8</td>
<td>0.11046</td>
<td>0.54</td>
<td>0.817</td>
</tr>
<tr>
<td>Error</td>
<td>30</td>
<td>0.76660</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Single parasitized eggs</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parasitoid age</td>
<td>2</td>
<td>0.02225</td>
<td>0.38</td>
<td>0.690</td>
</tr>
<tr>
<td>Host egg number</td>
<td>4</td>
<td>0.45745</td>
<td>3.87</td>
<td>0.012</td>
</tr>
<tr>
<td>Parasitoid age × Host egg number</td>
<td>8</td>
<td>0.03941</td>
<td>0.17</td>
<td>0.994</td>
</tr>
<tr>
<td>Error</td>
<td>30</td>
<td>0.88680</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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_{Emergence Rate} = 0.822, P_{Superparasitized Egg} = 0.817, P_{Single Parasitized Egg} = 0.994) (Table 1). The highest percentage parasitoid emergence was recorded for 5 day old parasitoids (126%) and 5 host eggs (135.5%). 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. The statistical results are shown in Table 2. 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_{Emergence Rate} = 0.822, P_{Superparasitized Egg} = 0.817, P_{Single Parasitized Egg} = 0.994) (Table 1). The highest percentage parasitoid emergence was recorded for 5 day old parasitoids (126%) and 5 host eggs (135.5%). 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).

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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 & Ghaioule, 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; Ttsanok 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; Wanberg 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 hosts (van Dijken & Waage, 1987; van Alphen & Visser, 1990; Visser et al., 1992; Metcalfe & 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 Leptomelaina heterotoma (Hymenoptera: Eucoilidae) (Visser, 1993) can recognize parasitized hosts. Strand (1986) reports that Telenomus holothisis (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, Potting 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, Doly cocor haccarum, Rhaphigaster nebulosa, Eurydemena 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 Aphaca nta genevensis (Hymenoptera: Braconidae) normally lays one egg per host, but two or more offspring can successfully complete their development when superparasitism occurs.
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 niten* (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 *Ventricula 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 & Kilincer (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**


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