

Effect of superparasitism on the development of the solitary parasitoid *Chelonus oculator* Panzer (Hymenoptera: Braconidae)

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Abstract: The egg-larval parasitoid *Chelonus oculator* Panzer (Hymenoptera: Braconidae) is a solitary endoparasitoid. The effect of superparasitism on the development of *C. oculator* was investigated on a host, *Cadra cautella* Walker (Lepidoptera: Pyralidae) at 25 °C, 60%-70% R.H., and 16:8 h (L:D) photoperiod. The development time of *C. oculator* from egg to adult was related to parasitism level from 42.5 ± 0.19 days under single parasitism to 48.4 ± 0.57 days under triple parasitism. The emergence rate of the parasitoid decreased as the parasitism level increased. In addition, the dry mass of adult parasitoid was significantly affected by the superparasitism. Consequently, for *C. oculator* developing in the host *Cadra cautella*, superparasitism has a negative effect on the quality of mass reared *Chelonus* wasps.

Key words: Solitary parasitoid, superparasitism, development, *Chelonus oculator*, *Cadra cautella*

Süperparazitizmin soliter parazitoit *Chelonus oculator* Panzer (Hymenoptera: Braconidae)'un gelişimine etkileri

Özet: Bir yumurta-larva parazitoiti olan *Chelonus oculator* Panzer (Hymenoptera: Braconidae) soliter endoparazitoittir. Süperparazitizmin *Chelonus oculator*'un gelişimine etkileri, konukçusu *Cadra cautella* Walker (Lepidoptera: Pyralidae) üzerinde 25 °C sıcaklık, % 60-70 oranlı nem ve 16:8 saat (aydınlık:karanlık) koşullarında belirlenmiştir. *C. oculator*'un yumurtadan ergin dönemine kadar olan gelişme süresi parazitizm derecesiyle ilişkili olup bu süre tek yumurta bırakılan parazitilemede 42.5 ± 0.19 gün, üç yumurta bırakılan parazitilemede ise 48.4 ± 0.57 gündür. Parazitoitin çıkış oranı parazitleme derecesi arttıkça azalmıştır. Ayrıca parazitoitin ergin büyüklüğü süperparazitizmden önemli derecede etkilenmiştir. Sonuç olarak konukçusu *Cadra cautella* üzerinde gelişen *C. oculator* için süperparazitizm, parazitoitin kitle üretiminde olumsuz bir etkiye neden olmaktadır.

Anahtar sözcükler: Soliter parazitoit, süperparazitizm, gelişme, *Chelonus oculator*, *Cadra cautella*

Introduction

Superparasitism, the deposition of an egg or eggs by a parasitoid into or on a host that has already been parasitized with one or more eggs, is commonly

reported in field and laboratory studies (Salt, 1961). In solitary parasitoid species, only one larva survives in each superparasitized host. If multiple eggs are present the parasitoids must compete for possession

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of the host, variously by ovicide, interlarval fighting, or physiological suppression (Salt, 1961; Fisher, 1963; Vinson and Hegazi, 1998). Because of superparasitizing the female may waste search time and eggs; this behaviour has often been considered maladaptive (Gardner et al., 1984). However, recent studies have shown that the allocation of additional eggs to an already parasitized host may be beneficial under certain conditions (van Alphen and Visser, 1990; van der Hoeven and Hemerik, 1990; Visser et al., 1990). A female may gain in fitness by ovipositing in an already parasitized host if the probability that her progeny will survive is greater than zero and if unparasitized hosts of equal or higher quality are not available (Bai and Mackauer, 1992). Models of superparasitism as an adaptive strategy (van der Hoeven and Hemerik, 1990; Visser et al., 1990) include the implicit assumption that superparasitism by a solitary wasp has no fitness consequences for the surviving larva, for example in terms of increased development time or reduced adult size. Whyllie (1983) showed that larvae of the solitary parasitoid *Microtonus vittatae* required longer time to complete development in superparasitized than in single parasitized chrysomelid beetles.

Many solitary parasitoids are able to discriminate between healthy and parasitized hosts (Bakker et al., 1985; Salt, 1961; Volk and Mackauer, 1990). This discrimination is possible because parasitoids often mark a host that they attack (Roitberg and Mangel, 1988). Additionally, some parasitoids can also discriminate between hosts parasitized by them or by another conspecific (Hubbard et al., 1987; van Dijken et al., 1992). With a solitary parasitoid a gain in fitness from self-superparasitism is not likely and is a waste of oviposition time and eggs. Conspecific superparasitism can be advantageous under a wider range of conditions, due to the possibility of eliminating a nonsib competitor from the parasitized host (van Alphen and Visser, 1990).

The effects of superparasitism show differences in koinobiont and idiobiont parasitoids. In contrast to idiobionts, which develop in non-growing or paralyzed hosts, the host of the koinobiont continues to feed, grow, and metamorphose during the initial parasitism. In koinobiont associations, host quality is not a linear function of host size but varies with future

host growth, which depends on the host stage at parasitization (Sequeira and Mackauer, 1992).

The solitary koinobiont egg-larval parasitoid, *Chelonus oculator* Panzer (Hymenoptera: Braconidae) was able to parasitize important lepidopterous pests (*Agrotis segetum* Denis & Schiffermüller, *Helicoverpa armigera* Hübner, *Heliothis virescens* Hufnagel, *H. peltigera* Denis & Schiffermüller, *Spodoptera exigua* Hübner, *Photodes elymi* Treitschke (Lepidoptera: Noctuidae), *Etiella zinckenella* Treitschke (Lepidoptera: Phycitidae), *Pyrausta sticticalis* (L.) (Lepidoptera: Pyraustidae), *Coleophora anatipennella* Hübner (Lepidoptera: Coleophoridae), and *Zeiraphera isertana* (F.) (Lepidoptera: Tortricidae). *Spodoptera littoralis* Boisduval (Lepidoptera: Noctuidae), *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae), and *Cadra cautella* Walker (Lepidoptera: Pyralidae) were described as new hosts for the parasitoid (Özkan and Özmen, 2001; Özmen et al., 2002; Ozkan and Tunca, 2005).

The reproduction of the parasitoid is arrhenotokous, in which only male progeny develop parthenogenetically from unfertilized (diploid) eggs, and male and female progeny develop from fertilized (diploid) eggs. The eggs are laid in the host eggs singly. They hatch in the host eggs, and first and second instar of the parasitoid feed internally. In its third instar, the parasitoid larvae leave the host to feed externally, consuming all except the skin and head capsule. The parasitoid then spins its cocoon in the pupal cell previously prepared by the host larva (Özkan and Özmen, 2001). In the present study, the effects of superparasitism on parasitoid development, emergence rate, and size were examined in eggs of *Cadra cautella* under single, double, and triple parasitism.

Materials and methods

Rearing of *Cadra cautella*

Cadra cautella (Walker) (Lepidoptera: Pyralidae), used in these experiments as host, were derived from a standard laboratory culture. *C. cautella* was reared in a climate room providing 25 ± 1 °C temperature, 60%-70% R.H., 16:8 h (L:D) photoperiod. In the rearing of *C. cautella*, wheat bran, corn flour, dry yeast, honey, milk powder, and glycerin were mixed in a ratio of

2:1:0.25:0.50:0.25:0.25, respectively. Before using the mixed preparation, it was kept in an incubator. Sterilized plastic breeding containers 15 × 20 × 7.5 cm in size were filled with 300 g of sterilized food and over this nearly 400 0- to 24-h-old *C. cautella* eggs were homogeneously dispersed using a soft tip brush. The containers were kept in the climatized rearing room during the study. Adult moths were collected with the help of an aspirator and transferred into ovipositing cages. For the continuity of the culture, a new culture was established every day using *C. cautella* eggs, collected every 24 h (Ozkan and Tunca, 2005).

Rearing of *Chelonus oculator*

The parasitoid was reared at 25 ± 1 °C, 60-70% R.H., and 16:8 h (L:D) photoperiod. Eggs obtained from the *C. cautella* culture were used for production. Approximately 400 24- to 48-h-old eggs of *C. cautella* were stuck on a paper sheet (4 × 15 × 10 cm) with the help of 5% Arabic gum solution, and put together with the fed and reproduced parasitoids located in a 10-L glass jar. Honey, as a necessary food for adult parasitoids, was spread over the paper strips carrying *C. cautella* eggs. Host eggs, which were served to parasitoids for 24 h, were transferred to plastic containers (15 × 20 × 7.5 cm) containing 300 g of sterile food (Ozkan and Tunca, 2005). This procedure was repeated every day. Adult parasitoids were utilized both for the existing experiments and for the set-up of the parasitoid culture.

Superparasitism

All laboratory experiments were performed at 25 °C, 60-70% R.H., and 16:8 h (L:D) photoperiod. In the experiments 0- to 24-h-old eggs of *C. cautella* and 3- to 4-day-old adults of *C. oculator* were used. In previous studies the time interval between ovipositions was 18 h (Tunca, 2005).

In order to obtain singly parasitized host a single wasp was put together with 100 host eggs in petri dishes (9 cm). The parasitoids were observed during oviposition until the characteristic parasitization behavior.

If the egg was rejected by the parasitoid, the host egg was eliminated. After being parasitized the host eggs were placed in glass vials with excess food until parasitoid eclosion. Four hundred host eggs were singly parasitized.

To obtain superparasitized hosts *C. cautella* eggs that had been parasitized once were presented to a conspecific parasitoid 18 h later. The wasps were again observed during oviposition, and superparasitized eggs (2 and 3 eggs per host) were immediately placed into vials with excess food until parasitoid eclosion. As a result 215 host eggs were parasitized twice and 80 host eggs were parasitized 3 times.

Adult wasp eclosion was checked twice during the day, which enabled development times to be accurately recorded. By using collected data, at each parasitism level, development time and adult emergence ratio of the parasitoid were determined. In order to determine parasitoid dry mass (mg), they were frozen upon emergence and later oven-dried for 5 days at 60 °C (Harvey et al., 1993).

Data analysis

Data on development time and adult dry mass were subjected to one-way analysis of variance (ANOVA) and significant differences were identified using Duncan's multiple range test. Percentages were transformed to arcsine values before ANOVA. All the analyses were carried out at the 5% significance level.

Results

Superparasitism had a significant effect on the development time of *C. oculator* ($df = 2$, $F = 69.80$, $P < 0.05$) (Figure 1). The development time of the parasitoid decreased as the parasitism level increased. The developmental of the parasitoid was 42.5 ± 0.19 days under single parasitism, while its

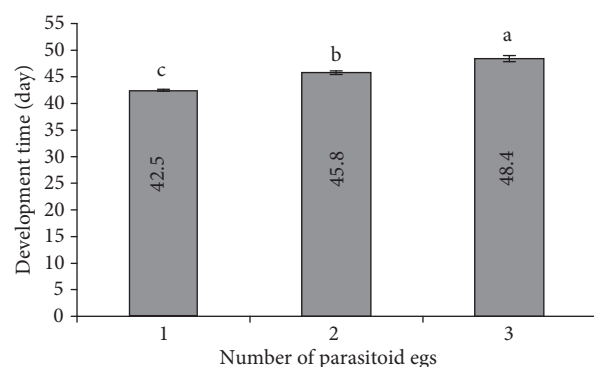


Figure 1. Development time of *Chelonus oculator* under single parasitism and superparasitism.

development was 48.4 ± 0.57 days under triple parasitism (Figure 1).

Similarly, emergence rate of the parasitoid decreased as the parasitism level increased ($df = 2, F = 30.11, P < 0.05$) (Figure 2). The adult emergence rate of *C. oculator* obtained under singly parasitism was much higher (63.2%) than that obtained under double and triple parasitism (42.7% and 37.5%, respectively).

There were significant difference between the dry mass of the parasitoid in single parasitism and superparasitism ($df = 2, F = 6.08, P < 0.05$) (Figure 3). However, the dry mass of the parasitoids did not significantly differ from each other under double and triple parasitism.

Discussion

The results indicated that the development time of the parasitoid was significantly prolonged under superparasitism and a longer duration was observed under triple parasitism (Figure 1). Comparison of the development of *C. oculator* in single parasitized and superparasitized *C. cautella* revealed that superparasitism resulted in a lower rate of adult emergence (Figure 2). This was probably due to the fraction of interlarval contests in which both parasitoids die. Several researchers have already reported that development times of the parasitoid species change depending on superparasitism. Superparasitism affects subsequent parasitoid development and has been suggested as a factor leading to extended emergence periods in several

Trichogramma species (Parra et al., 1988). Similarly, Gerling (1972), Eller et al. (1990), Simmonds (1943), Whyllie (1983), and Vinson and Sroka (1978) reported that development times of *Telenomus remus*, *Microptilis croipes*, *Venturia canescens*, *Microtonus vittatae*, and *Cardiochiles nigriceps* increased under superparasitism.

Development time of *Tiphodytes gerriphagus* Marchal (Hymenoptera: Scelionidae) in superparasitized eggs was longer than that of the parasitoid under single parasitism (Sousa and Spence, 2000). Harvey et al. (1993) studied the effect of superparasitism on the development of the solitary endoparasitoid *V. canescens* on different instars of *Plodia interpunctella* Hübner (Lepidoptera: Pyralidae). They found no significant differences in development time from third instar hosts containing 1 or 2 eggs, but parasitoids developing in fifth instar hosts containing 2 eggs displayed a longer development time.

González et al. (2006) reported that adult parasitoid emergence (*Diachasmimorpha longicaudata*) decreased as the level of superparasitism increased. Similarly, Santolamazza-Carbone and Cordero-Rivera (2003) reported that the emergence rate of *Anaphes nitens* decreased as the number of eggs per host increased. This situation was explained by physical combat among early instar larvae. Vinson et al. (1987) investigated a similar decrease in the emergence rate of parasitoid with egg number for the braconid parasitoid *Cardiochiles nigriceps* attacking the tobacco budworm *Heliothis*

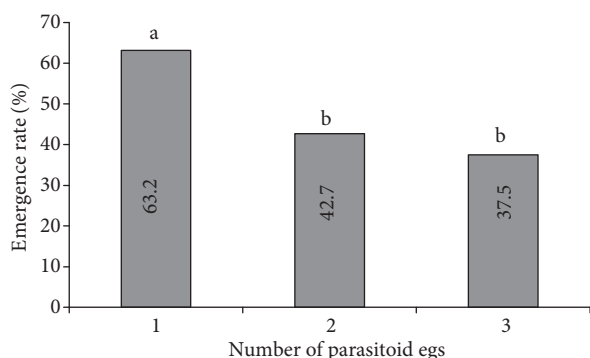


Figure 2. Emergence ratio of *Chelonus oculator* under single parasitism and superparasitism.

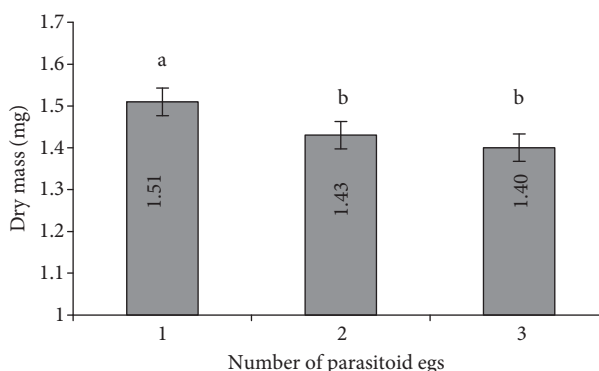


Figure 3. Dry mass of *Chelonus oculator* under single parasitism and superparasitism.

virescens Fabricius (Lepidoptera: Noctuidae). Uğur (1996) observed that the mortality of *Pimpla turionella* increased under superparasitism with the host *Galleria mellonella*.

In addition, the dry mass of *C. oculator* from superparasitized hosts was smaller than that of parasitoids from singly parasitized hosts (Figure 3). Potting et al. (1997) and Santolamazza-Carbone and Cordero-Rivera (2003) found that the *Cotesia flavipes* and *Anaphes nitens* from superparasitized hosts were smaller than parasitoids from singly parasitized hosts. This situation was explained by scramble competition for host resources. Similarly, Ozkan (2006) show that superparasitism significantly decreased the size of *C. oculator* in both host diet treatments on *Ephestia kuehniella*.

However, Bai and Mackauer (1992) found that *Aphidius ervi* from superparasitized pea aphids were significantly larger than those from singly parasitized aphids. They stated that this was because

superparasitized aphids ingested more food and incorporated it more efficiently than singly parasitized and non-parasitized controls, in that order. In contrast, Uğur (1996) found no significant differences in the size of *Pimpla turionellae* under superparasitism.

In summary, it was found in the present study that the development period from egg to adult emergence increased under double and triple parasitism, and emergence rate and size of adults decreased under superparasitism. The results confirm that superparasitism of the target host has a negative effect on the quality of mass reared *Chelonus* wasps.

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