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Copulation behaviour and reproduction of mated and unmated females of *Ooencyrtus pityocampae* (Mercet) (Hymenoptera Chalcidoidea Encyrtidae), an important egg parasitoid of the pine processionary moth

Abstract - From egg batches of *Thaumetopoea pityocampa* (Den. & Schiff.) collected on the Iberian Peninsula 5.4 -10.4% males of the egg parasitoid *Ooencyrtus pityocampae* (Mercet) emerged and copulated under laboratory conditions: Thus, copulation of the species could be studied in detail. For producing obspring, eggs of *Bombyx mori* L. and *T. pityocampa* were used. Mated females of the encyrtid produced only female offspring, since from eggs of virgin females both sexes developed. The honey-fed females lived maximally 56 days and laid 70 eggs per female at maximum. From 59% of the eggs laid female offspring emerged after 21 days. About 11, maximally 38, offspring individuals per female were observed. Totally, in 668 offspring specimens the male part was 2.7%. The diapausing individuals were not considered.

Riassunto - *Accoppiamento e riproduzione di femmine fecondate e vergini di* Ooencyrtus pityocampae *(Mercet) (Hymenoptera Chalcidoidea Encyrtidae), un importante parassitoide oofago della processionaria del pino.*

Da ovature di *Thaumetopoea pityocampa* (Den. & Schiff.) raccolte nella Penisola Iberica, 5.4-10.4% di maschi del parassitoide oofago *Ooencyrtus pityocampae* (Mercet) sono sfarfallati e si sono accoppiati in laboratorio. Per l'ovideposizione sono state utilizzate uova di *Bombyx mori* L. e *T. pityocampa.* Le femmine fecondate dell'Encirtide hanno prodotto solo femmine, mentre dalle uova delle femmine vergini sono nati individui di entrambi i sessi. La maggiore sopravvivenza delle femmine alimentate con miele è di 56 giorni, con un massimo di 70 uova deposte per femmina. Dal 59% delle uova deposte sono schiuse femmine dopo 21 giorni. Sono state osservate da 11, ad un di massimo 38 individui per femmina. Complessivamente su 668 individui nati i maschi costituiscono il 2.7%. Gli individui in diapausa non sono stati considerati.

Zusammenfassung - *Kopulationsverhalten und Reproduktion von* Ooencyrtus pityocampae *(Mercet) (Hymenoptera Chalcidoidea Encyrtidae), ein bedeutender Eiparasitoid des Pinienprocessionsspinners.*

Aus Eigelegen des Pinienprozessionsspinners *Thaumetopoea pityocampa* (Den. & Schiff.), die an verschiedenen Gegenden der Iberischen Halbinsel gesammelt wurden, schlüpften 5,4-10,4 % Männchen des Eiparasitoiden *Ooencyrtus pityo-*

campae (Mercet), die unter Laborbedingungen mit den zur gleichen Zeit geschlüpften Weibchen kopulierten, so daß das Kopulationsverhalten im Detail beobachtet werden konnte. Um Nachkommen zu erhalten, wurden den Eiparasitoiden zur Reproduktion Eier von *Bombyx mori* L. und *T. pityocampa* angeboten, die sogleich parasitiert wurden. Begattete Weibchen produzierten nur weibliche Nachkommen, während aus Eiern virginer Weibchen sich beide Geschlechter entwickelten. Die encyrtiden Weibchen lebten maximal 56 Tage mit Honig und legten maximal 70 Eier pro Weibchen. Lediglich von 59% der abgelegten Eier schlüpften Nachkommen nach frühestens 21 Tagen, im Mittel 11 (max. 38) Nachkommen pro Weibchen. Von den insgesamt erhaltenen 668 Nachkommen betrug der Männchenanteil 2,7%. Das Schicksal der diapausierenden Individuen wurde nicht weiter verfolgt.

Key words: *Ooencyrtus pityocampae*, Encyrtidae, egg parasitoid, copulation behaviour, oviposition, reproduction, male offspring.

INTRODUCTION

Ooencyrtus pityocampae (Mercet) is one of the most effective solitary and primary egg parasitoids of the pine processionary moths, *Thaumetopoea pityocampa* (Den. & Schiff.) and *T. wilkinsoni* Tams, which are known as most important pine pests widely distributed in South Europe, North Africa and Asia Minor, summerised by Schmidt (1990b). In order to reduce or avoid the application of unspecific chemical pesticides as control method (summarized by Schmidt *et al.*, 1998). Halperin (1970) was the first who used ooparasitoids for the control of the pine processionary moth in Israel, but he was less successful due to the great number of diapausing individuals, not favourable for the development of more them two generations per host generation. First, the biology of the egg parasitoids, their impact on and the multiplication methods had to be studied in detail (Masutti, 1964; Tiberi, 1978; Geri, 1980; Battisti, 1989; Schmidt, 1990; Bellin, 1994; Tsankov *et al.*, 1996a). All the observations and investigations came to the result that the encyrtid was the most frequent and active ooparasitoid which can be bred also in eggs of other insects (Lepidoptera and Heteroptera) than of *Thaumetopoea* eggs (Halperin, 1990) and that it is possible to use deep frozen unfertilized eggs for breeding (Schmidt & Kitt, 1993). In nature, the egg parasitoid prefers eggs of alternative hosts, if they were laid in rows or groups of 10-25 eggs on pine needles and without scale protection (Tiberi, 1988).

As main facultative egg parasitoid of *Thaumetopoea* spp., the distribution of *O. pitÿocampae* covers the whole region of the host, especially the mediterranean part from Israel to Morocco and in southern Europe from Greece-Bulgaria to Spain-Portugal. Its generations are not well synchronized with those of the main host, thus alternative hosts are needed to retain the connection with the next main host generation (Garcia-Fuéntes, 1965, Battisti *et al.*, 1988).

The very small and metallic shining encyrtid can produce several generations per year depending on the climate and the periods of main host oviposition (Halperin, 1990; Bellin *et al.*, 1990; Kitt & Schmidt, 1993; Tsankov *et al.*, 1996a,b) and can cause a mortality impact on the pine pest up to 34% in Bulgaria (Tsankov *et al.*, 1998) and up to 46% in Italy (Tiberi, 1978). The adults are able to emerge after 2-3 weeks and parasitize again on adequate eggs. Other individuals go in diapause and hibernate in the eggs as mature larvae for emergence in the following year (Halperin, 1990; Tsankov *et al.* 1996b).

The reproduction of *O. pityocampae* occurs mainly unisexuell thelythokous (Halperin 1970, 1990; Battisti, 1989; Schmidt *et al.*, 1997a,b). Males appeared very seldom (Kailidis, 1962; Graham, 1991; Ben Jamaa, 1992; Bellin, 1994). In Isreal, 0.6% males were found (Kitt & Schmidt, 1993). Tsankov *et al.* (1998) found maximally 1.0-4.8% males in Bulgaria. Battisti *et al.* (1990) detected only one male under about 3000 female individuals. Therefore, we were lucky to observe much more adult males in a recent study of the egg parasitoids from the Iberian Peninsula (Schmidt *et al.*, 1999), that led us to detailed observations of the copulation behaviour and to study the mating effect.

MATERIALS AND METHODS

The egg batches of *T. pityocampa* (Den. & Schiff.) were collected at four regions on the Iberian Peninsula: I. Sierra Nevada, II. Sierra de Alberracin, III. near Vila Real/ Portugal and IV. near Jaca/Pyrenees (Schmidt *et al.*, 1999). Directly after collection the egg batches were singled in plastic vials of 6.5 ml, closed with foam stoppers and hold at 20-25°C, under laboratory conditions. Following numbers of egg batches were evaluated for emergence of *O. pityocampae* males and females:

I. Sierra Nevada, near the Passa Puerto de la Ragua in about 1700 m a.s.l., 147 egg batches were found on *Pinus halepensis*. The nearest city to the North was Lacalahorra, near Guadix. The egg batches were collected on 11.VIII.1991, shortly before caterpillars' hatch which occurred from 12.VIII. to 14.VIII.1991.

II. Sierra de Alberracin, near Teruel about 80 km from Valencia at 1500 m a.s.l. on 20.VIII.1991, shortly after caterpllars' hatch, 17 egg batches were collected on *Pinus halepensis*.

III. Vila Real/Portugal, about 80 km to the East of Oporto at 500 m a.s.l. on 29.I.1992, 31 egg batches were sampled on *Pinus pinaster* deposited in 1991; the hatching period of the caterpillars took place in late summer 1991.

IV. Near Jaca in the Pyrenees, near Hostal de Ipies at about 800 m a.s.l., 21 egg batches were found on *P. halepensis* on 30.VIII.1992; near Aisa at Loma de Cajicar at 1300 m a.s.l., 30 egg batches were sampled on *P. halepensis* on 1.IX.1992, and to the West of Jaca in direction to Pamplona, near a damed-up lake in the Sierra Legre/Corral de Embain, at 650 m a.s.l. 27 egg batches were collected. All batches were sampled shortly after the hatching of the caterpillars. In total, 78 egg batches were studied at region IV.

After collection, the emergence of the egg parasitoids were counted almost daily, the emergent individuals were removed from the vials and sexed for further studies. Observations of their behaviour and copulation were carried out. In April to June, female individuals were paired singly with males of the various localities in plastic vials provided with drops of honey solution. Each pair was observed for 20 min and the behaviour registered in detail. 35 repititions were performed followed by breeding experiments with mated and unmated females singled in vials of similar size, as mentioned above, closed with foam stoppers. Also these vials were kept at room temperature of 20-25°C. The foam stoppers were moistened every second day. As food, the encyrtids were offered small honey drops and for oviposition frozen eggs of *Bombyx mori* L. and eggs withdrawn from deep frozen Greek *T. pityocampa* females without cleaning. The eggs were scattered on small Bristol paper strips (10 x 20 mm) glued with wallpaper paste and placed inside the vials. Observations were done on host feeding, acceptance of the *Bombyx* eggs as alternative host eggs in comparison to *T. pityocampa* eggs and the starting of oviposition. Honey drops were replaced and further host eggs were offered every second day until females death.

Oviposition of the females was observed by the appearence of the respiratory mask, characteristic of the encyrtid, similar to a cap sticked to a thin respiratory pipe marking the place of egg laying (Tanzen & Schmidt, 1995).

The emergent offspring was counted during several weeks, until no adults appeared. The diapausing larvae were not considered.

RESULTS

1. Behavioural observations

Released inside the plastic vials, the insects started first cleaning their bodies, especially the antennae were cleaned extensively. After some minutes they moved around the tube walls, the females were more active than the males. The latter often stopped moving and spread their hairy antennae sidewards forming a 'V' (Fig. 1). All insects found the honey drop very soon and fed on it. After feeding, the females started again running, since the males needed much more time for cleaning.

2. Copulation behaviour

After pairing, the cleaning behaviour started again immediately. The female moved first followed by the male. Meeting of the pair induced the activity of the male running behind the female and trying to touch her with his antennae. Sometimes refusing wing movements of the female were observed. The wings were angled sidewards and lifted. The male stopped moving immediately, but started again approaching the female after some seconds. If the male touched the female from behind again, the movements of the female became clearly slowlier. Then, the male passed the female sidewards and both placed themselves head by head. Then, the male started waving

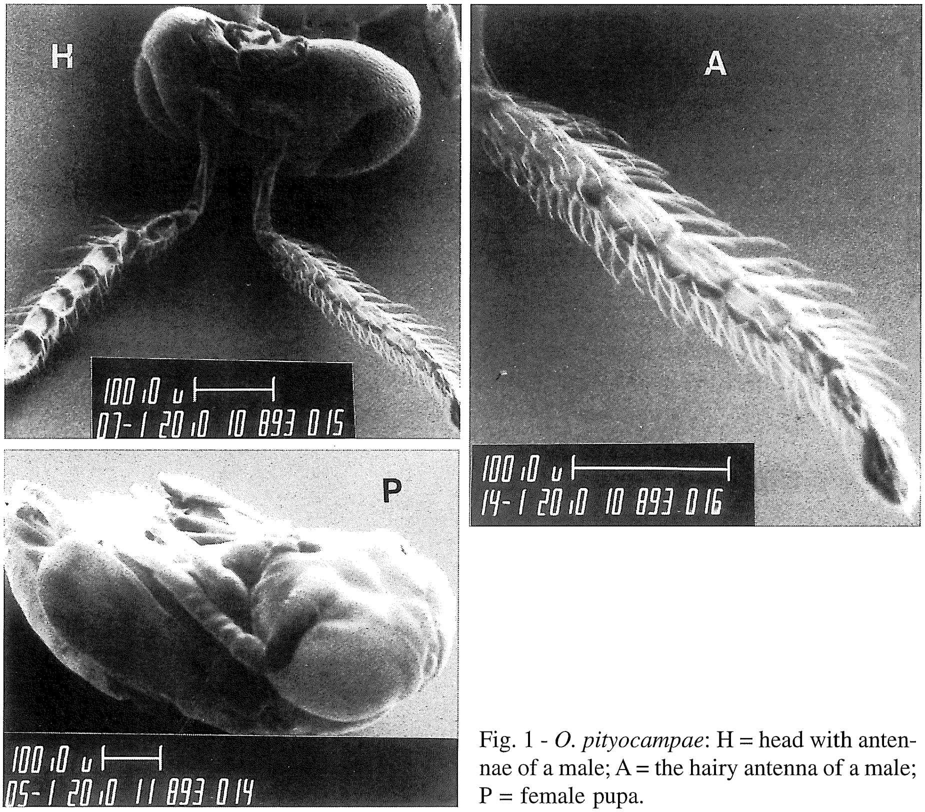

Fig. 1 - *O. pityocampae*: H = head with antennae of a male; A = the hairy antenna of a male; P = female pupa.

the front parts, head and thorax, of the body from left to right and reverse, whilst the male tapped the female with his antennae. If the female stopped moving, copulation started immediately. After copulation the male began again in waving head and thorax and tapping the female. The pair left another without transition behaviour and started cleaning after 10 to 20 sec..

Not every meeting of the individuals was followed by a copulation. Partly, the male was rejected for the first time and copulation occurred at the second turn. In some cases, it could be observed that the female copulated several times with the male within 20 minutes.

3. *Reproduction of offspring*

Both paired and virgin females were bred and the adult offspring counted. The females accepted unfertilized eggs from *T. pityocampa* as well as eggs from *Bombyx mori*. In the first two days after offering host eggs no oviposition could be observed, although the host eggs were extensively proved by the females. Partly, it could be observed that the female tapped a host egg by the ovipositor and fed on the exuded liquid. Sometimes the female tapped twice to obtain more liquid.

On the third day the females started to parasitize the host eggs. This was clearly visible by the respiratory pipe.

The offspring of 14 mated and 46 virgin females was evaluated. The females laid eggs until their death. The adult lifespan was maximally 56 days (8 weeks) per female, a mean lifespan of 17 days was found; some females survived only few days. The number of eggs laid correlated with the age of the female (Fig. 2).

The mean oviposition rate per female was 18.7 eggs, maximally 70 host eggs were parasitized by one female. Each parasitized host egg contained only one encyrtid egg. About 11 days after parasitation the first meconium was visible in the eggs and after 21 days the first offspring appeared. From the deposited encyrtid eggs, 59.4% offspring emerged, the rest of the eggs developed dead stages and alive larvae, not yet pupate. Differences between mated and unmated females could not be observed.

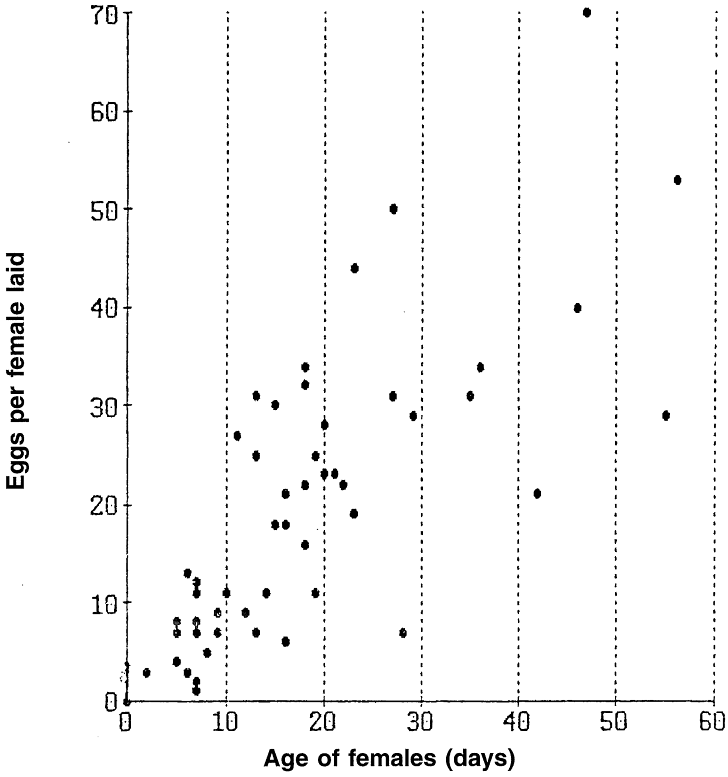

Fig. 2 - Female age in relation to egg production per female in *O. pityocampae*.

The mated females produced exclusively female offspring. From eggs of unmated females, males and females emerged. The 18 males found in the offspring originated from 14 virgin females.

In total, the 6o females used for parasitism produced 668 offspring specimens, from which 97.3% were females, and only 2.7% males were found as adults emerged. As mean, each female produced 11 adults by spontaneous development, maximally 38 offspring individuals per female were counted. A spontaneous development were found in *T. pityocampa* eggs as well as in *Bombyx* eggs.

DISCUSSION

To our knowledge, this paper presents the first report on the copulation behaviour of the encyrtid *O. pityocampae* as ooparasitoid of the pine processionary moth. Males can be identified easily by their hairy antennae. The very low percentage of males found in most of the populations studied had made it difficult to perform mating experiments.

Our experiments show that mating has no effect on the lifespan of the females and egg production, which depends on the lifespan of the adult females and the food offered. The lifespan of the females is very variable and depends mainly on the temperature in which they lived (Halperin, 1970, 1990). At room temperature we observed that some females didn't produce eggs and died after some days, in spite of feeding on honey drops and water. On the other hand, females can produce some eggs without taking food, and egg laying increased when the females could puncture an host egg to obtain some yolk proteins (Battisti *et al.*, 1990).

In nature, the females will take honey-dew, produced by aphids all over there, to survive for several weeks and to produce offspring when host eggs are avaible. Under laboratory conditions, 50% of the females survived five weeks at 15°C (Kitt & Schmidt, 1993). In the present experiments, a mean lifespan of 17 days was found at 20-25°C. Halperin (1990) reported up to 90 days at 19°C and only 30-35 days at 27-30°C for the lifespan of the species outdoors in September-November in Israel. The results show that the lifespan of *O. pityocampae* is clearly shortened by increasing temperature, although food and water were offered ad libitum, in every case.

Mated and virgin females accepted not only eggs of *T. pityocampa* but also eggs of other Lepidoptera (e.g. *Bombyx mori*) without showing any difference in the behaviour, and oviposition takes place in unlaid as well as deposited eggs of the main host, as reported first by Schmidt & Kitt (1993). The eggs must not be placed in batches or groups, as mentioned by Tiberi (1988), they can be scattered also on a paper board. Most important for the acceptance of the eggs seems to be their size as referred by Halperin (1990), a chemical trigger could not be observed. Tsankov *et al.* (1998) found outdoors that sterile host eggs can be parasitized (up to 45%) as well as embryonic stages. The encyrtid cannot discriminate between fertilized and sterile host eggs as demonstrated also in our experiments in which up to 70 unfertilized eggs were parasitized by one female, since Halperin (1990) found that one single female can deposite a mean of 27 (8-47) eggs. This may be favoured by the unscaled eggs used by us in all the cases, for it is known that the encyrtid prefer unscaled eggs for parasitation (Biliotti, 1958; Masutti, 1964; Halperin, 1970, 1990; Kitt & Schmidt, 1993). Superparasitism was not observed.

Freshly laid and unlaid eggs are most favourable for oviposition of the encyrtid resulting in successful development, but also some mortality was observed (Halperin, 1990). In *Ooencyrtus nezarae* Ishii oviposition decreased with increasing age of the host eggs (Takasu & Hirose, 1993). In nature two generations of *O. pityocampae* can develop in a single egg cluster, if oviposition starts at the beginning of host egg deposition and lasts for several weeks. The higher the temperature the more eggs were laid daily, but the oviposition period is shortened as mentioned above. In our case, oviposition continued about 14 days at 23°C and after Halperin (1990) it lasted only 2-4 days at 33°C, with an oviposition rate of 19 eggs per day at 35°C. Battisti *et al.* (1990) counted a maximum of 42 eggs laid per female in the laboratory.

Under our breeding conditions a maximal female lifespan of 56 days was registered, since Battisti *et al.* (1990) found a lifespan of 45 days at standard laboratory conditions.

At 22-25°C the larval development reached the prepupal stage after 11 days when the meconium became visible (Masutti *et al.*, 1992, 1993). The first adults emerged three weeks after oviposition according to Masutti (1964), Halperin (1970, 1990), Battisti *et al.* (1992) and Tsankov *et al.* (1996b).

Unlaid eggs of *T. pityocampa* exposed to *O. pityocampae* were easily parasitized up to 66% in spring and 53% in autumn under laboratory conditions. From eggs parasitized in May, adults emerged at two periods, the first group appeared after 3-4 weeks and the second after some month in August-September. From eggs parasitized in October, adults emerged first in the spring of the following year (Schmidt & Kitt, 1995); all adults were females. In the present study, when the eggs were parasitized at springtime (April to June), about 60% of the encyrtid eggs underwent a spontaneous development reaching the adult stage after three weeks. In nature on the Iberian Peninsula, 60.7 to 96.8% of the encyrtid developed to adults before hibernation depending on the region and season in which the egg batches were collected (Schmidt *et al.*, 1999).

In spite of the eggs laid under similar ecological conditions, a high percentage can develop diapausing larvae from eggs laid by mated as well as unmated females. Under the same climatic conditions, some larvae developed faster than others in the host eggs independent from the temperature. Also males and females can develop from unfertilized encyrtid eggs under the same climatic conditions which contrasts the suggestion of Halperin (1970, 1990) that temperatures above 32°C are needed to develop males. Also, temperatures below 15°C are not necessery to induce a diapause. Tsankov *et al.* (1996b) reported from outdoor conditions that manifold parasitism of the same egg batch and at the same time in June can result in developing diapausing and non-diapausing larval stages.

After Flanders (1946) high temperatures are necessary to induce arrhenotokous parthenogenesis in unisexuell organisms in the parental generation. This agrees with the findings of Halperin (1990) that in females bred at 34°C and transferred for oviposition to 30°C, the first part of the offspring were males, following by males and females and finally females only. Sex determination by temperature was found being most important also in *Ooencyrtus submetallicus* (How.) in Australia (Wilson & Woolcock, 1960).

In the present study, 2.7% males of the total offspring emerged from eggs laid by unmated females under temperature conditions, in which exclusively females shall develop. Our experiments showed that the temperature cannot be responsible for male production only. No special females were responsible for male production, because the 18 adult males, observed in our study, developed from eggs laid by 14 virgin females. For male production, the observation of Tiberi (1988) may be of some interest that the percentage of males develop in eggs of Heteroptera in August-September was relativey high (♂♂:♀♀ = 17:72).

Since *O. pityocampae* males were accepted by the females and copulation appeared, a bisexual reproduction cannot be excluded in nature. In our study, mated females produced exclusively female offspring as it was found in arrhenotokous reproduction, in which males develop only from unfertilized eggs and females from fertilized ones. In Morocco, populations of *O. pityocampae* were found in that unmated females produced exclusively male offspring. From eggs laid by mated females both sexes appeared in the ratio ♂♂:♀♀ = 1.1:1 (Bellin, 1994). In such amphitokous reproduction the relation of male to female offspring can vary much, in which not exclusively the temperature is involved. Under this point of view, it shall be mentioned that mated and honey-fed *Trichogramma minutus* Riley (Chalcidoidea: Trichogrammatidae) produced exclusively male progeny (Leatemia *et al.,* 1995).

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