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Autor: Pittara, I.S. / Katsoyannos, B.I.

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Oviposition behavior, longevity, fecundity and fertility of *Chaetorellia australis* HERING (Diptera, Tephritidae)

I. S. PITTARA & B. I. KATSOYANNOS

University of Thessaloniki, Department of Agriculture, Laboratory of Applied Zoology and Parasitology, 540 06 Thessaloniki, Greece

We describe the oviposition behavior of *Chaetorellia australis* HERING (Diptera, Tephritidae) females caged in the laboratory with their natural oviposition substrates i.e. floral buds of yellow starthistle *Centaurea solstitialis* L. and *Centaurea cyanus* L. (Asteraceae, Cardueae). We also report laboratory studies on the longevity, fecundity, and fertility of the fly. We found that at 25° C the mean longevity of the males was 49.3 days and that of females was 33.7 days. The shortest preoviposition period observed was two days and about 85% of mated females began to oviposit the sixth day after emergence. Oviposition took place throughout the photophase and the oviposition period lasted about 50 days. During their life mated females laid on the average 74.9 eggs (maximum 242), with a mean hatchability of 90.5%, whereas virgin females laid on the average 11.6 unfertile eggs.

Chaetorellia HENDEL, a Western and Central Palearctic genus, belongs to the tribe Terelliini (Diptera, Tephritidae). The nine known *Chaetorellia* species attack the capitula of species of *Centaurea*, *Carthamus*, and *Chartolepis*, which are knapweeds and starthistles belonging to the subtribe Centaureinae (Asteraceae, Cardueae) (WHITE & MARQUARDT, 1989). The genus *Chaetorellia* was divided into the *C. loricata* (RONDANI) and *C. jaceae* (ROBINEAU-DESVOIDY) species groups by KORNEYEV (1985) on the basis of adult characters. These groups also differ in egg morphology and oviposition behavior (WHITE & MARQUARDT, 1989). *Chaetorellia australis* HERING, a member of the *C. jaceae* species group, is a potential biocontrol agent of the yellow starthistle (YST) *Centaurea solstitialis* L., a noxious weed originating from southern Europe and by 1985 covering about 7.9 million acres of pasture and other types of land in the Western USA (MADDOX, 1981; MADDOX & MAYFIELD, 1985; MADDOX *et al.*, 1985). SOBHIAN & ZWÖLFER (1985) and SOBHIAN & PITTARA (1988) give some information on the biology, oviposition behavior, and host specificity of *C. australis*, which is referred to by the above authors as *Chaetorellia hexachaeta* LOEW. According to them, the species has at least three generations per year in northern Greece. The overwintering generation pupates in YST floral buds. The emergence of adult flies starts in late April, when YST floral buds are not yet present in the field. Therefore, the females of that generation oviposit in buds of *C. cyanus* which, if that plant is available in the region, appear earlier than the YST buds. Matings start on the second day after emergence and oviposition on the following day. Usually one egg is deposited in each floral bud under its innermost bracts. Preliminary laboratory observations by SOBHIAN & ZWÖLFER (1985) and SOBHIAN & PITTARA (1988) indicated that the oviposition period of the fly lasted up to 60 days and up to 243 eggs were deposited by a single female.

In the present work we accurately describe the oviposition behavior of laboratory caged females and report the results of more extensive observations on the longevity, fecundity, and fertility of *C. australis*.

MATERIALS AND METHODS

The observations were conducted during the summer of 1986 in the laboratory at $25 \pm 2^\circ\text{C}$, $60 \pm 5\%$ r. h. and a L14 : D10 photoperiod, with the photophase between 06.00 and 20.00. Light was provided by nine fluorescent tubes of the daylight type and during most of the photophase also by natural daylight entering through two windows. The light intensity at the level of the cages containing the flies varied between 300 and 1200 lux, depending on the outdoor illumination.

The flies used had emerged from pupae originating from field infested seed heads of *C. solstitialis*, collected during the winter near Kilkis in northern Greece. The infested heads were stored in the refrigerator at 5°C , from which they were successively transferred to 25°C for fly emergence, depending on the needs.

For observations concerning the oviposition behavior, 5–15 day-old females were used. Before the observations started, the flies were caged in groups of 10–30 individuals of both sexes and daily provided with food (a dried mixture of yeast hydrolysate and sugar in a 1 : 4 proportion), water, and fresh YST buds suitable for the oviposition of the flies. For the observations, $34 \times 25 \times 25$ cm Plexiglas® cages were used, which had a 18 cm diameter wire-screen on the upper side. For each observation one female was transferred to a cage containing four uninfested floral buds of YST or *C. cyanus* suitable for oviposition (Bu-3 to Bu-4 for YST, as defined by MADDUX, 1981). The four buds, having stems of about 5 cm length, were placed with the proximal end of the stem in a 5 cm plastic vial containing water, and were positioned in such a manner that the stems formed an angle of about 45° to each other. The behavior of each female was continuously observed for 1–2 h and the number and duration of the visits to each bud, of the oviposition attempts without subsequent oviposition, and of the ovipositions, were recorded.

For observations concerning longevity, fecundity and fertility of virgin and mated females, and egg-laying activity during the photophase, the flies were caged upon emergence in pairs (a male and a female), or single females (virgins) in $15 \times 15 \times 15$ cm Plexiglas cages provided with food and water. Uninfested YST buds in Bu-3 to Bu-4 stages of development were used as oviposition sites, two in each cage, collected from an experimental field planted for this purpose near Thessaloniki. The buds in each cage were replaced every day by new uninfested ones and were dissected under a stereomicroscope to determine and count the number of eggs laid. The eggs, separately for each female and day, were placed on wet black filter paper in Petri dishes and after 3–4 days their hatchability was recorded. This procedure continued until the flies died. The mortality of the flies was recorded daily and dead flies were not replaced. To record the egg-laying activity during the photophase, mated, 6–14 day-old females were caged in groups of 4 individuals with 4 YST buds. The buds were replaced every two hours by new uninfested ones throughout the photophase. Then, the buds were dissected under a stereomicroscope and the number of eggs laid was recorded. This procedure was followed for two successive days, using the same females. The number of eggs laid by the females of a cage within each two-hour period was considered as a replicate.

Description of the oviposition behavior

Preliminary observations were conducted with females which either had not the opportunity to oviposit before the test, because no floral buds had been offered to them, or had been deprived of oviposition substrates for at least three days before the observations and hence presumably had a high oviposition pressure. These females attempted to oviposit almost immediately after a floral bud was offered to them and deposited more than one egg per bud during their first or even second visit to a bud. As many as four successive ovipositions into a bud during a single visit were observed. Usually after 5–6 ovipositions such females returned to normal behavior again, i.e. they deposited one egg per bud per visit.

The following description is based on individually caged, 5–15 day-old, mated females provided permanently with fresh, uninfested YST heads for oviposition and hence, presumably having a normal, moderate oviposition pressure. These females usually arrived on the buds by walking along the stem and rarely by flying. Once a female arrived on a YST (or *C. cyanus*) bud, three behavioral phases could be distinguished:

a) *Preoviposition phase*: The female walked slowly on the bud with the ovipositor pointing toward the substrate, and occasionally touched the surface with its proboscis, mostly at the edge of the bracts near the base of a spine. This apparent “search” for a suitable egg-laying site took place mostly in the apical part of a floral bud. If the bud had received an egg earlier, the female left it shortly after arrival ($\bar{x} = 20.7 \pm 16.7$ s, $N = 17$), usually by walking down the stem. If the bud was not infested, this search phase lasted much longer ($\bar{x} = 109.2 \pm 91.5$ s, $N = 9$).

b) *Phase of oviposition attempt(s) and oviposition*: After a female located a suitable site for oviposition, it turned its body around by about 180° and tried to insert its extended ovipositor between the bracts at the same site which it had previously touched with its proboscis. At that time, the female’s body formed an angle of about 90° with its ovipositor. Usually an egg was deposited after more than one oviposition attempt (i.e. boring not being followed by egg-laying), which lasted from 4 s to 2.9 min each ($\bar{x} = 36.6 \pm 35.9$ s, $N = 35$). During oviposition, which lasted from 1.2 to 3.6 min ($\bar{x} = 2.8 \pm 0.9$ min, $N = 30$), the female’s body also formed an angle of about 90° with its ovipositor.

c) *Postoviposition phase*: Immediately after egg-laying, the female withdrew its ovipositor from the bracts and began to drag it, at first around and very close to the oviposition point and then further and further away from it (Fig. 1). The walking of the female during dragging the ovipositor was more rapid than during the preoviposition search phase. The females behaved in the same manner on YST and on *C. cyanus* floral buds. In some cases the females dragged their extended ovipositor not only on the floral bud surface but also along a YST bud spine or even on the stem of the bud during their descent. Dragging was not always continuous, but in some cases was interrupted for a few to several seconds to clean the ovipositor with the metathoracic legs. The dragging behavior (including interruptions) lasted from 18 to 60 s ($\bar{x} = 38.1 \pm 32.3$ s, $N = 30$). In all but one of 200 ovipositions observed (verified by detecting the egg laid), the female performed ovipositor-dragging after egg-laying. After egg-laying and ovipositor-dragging, the female usually cleaned their ovipositor with their metathoracic leg tarsi, then

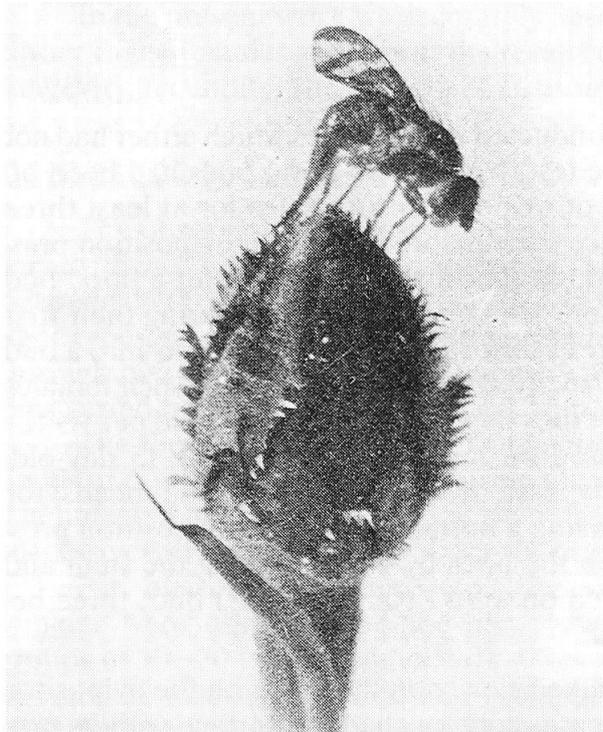


Fig. 1. *C. australis* female dragging its ovipositor on the surface of a *C. cyanus* floral bud, after oviposition.

Tab. 1. Egg-laying during the photophase in the laboratory (25° C). One replicate = eggs deposited from four *C. australis* females in two days at two-h intervals (N = 7).

Hours from the beginning of the photophase *	Eggs deposited		
	\bar{x} **	s	%
0 - 2	6.6	3.2	15.8
2 - 4	7.9	2.6	18.8
4 - 6	6.9	1.1	16.4
6 - 8	7.0	2.1	16.8
8 -10	5.1	1.5	12.3
10 -12	3.9	1.9	9.2
12 -14	4.4	3.5	10.6

* : Photophase between 06.00 and 20.00.

** : The mean numbers are not significantly different at the 5% level (WILCOXON-WILCOX test).

walked slowly on the bud and finally left it, usually by descending along the stem. Field observations showed that in nature the females behaved in the same manner as in the laboratory. We (PITTARA & KATSOYANNOS, 1990) were able to demonstrate that, similar to other tephritids (cf. AVERILL & PROKOPY, 1989) the females of *C. australis*, when dragging their ovipositor deposited a host-marking pheromone over the floral bud surface. This pheromone functions to prevent repeated oviposition in already infested buds and also plays a role in sexual behaviour by functioning as a male-arrestant.

Daily rhythm of oviposition

As shown in Tab. 1, the oviposition took place during the entire period of the photophase but a tendency for more intensive oviposition activity during the first eight hours of the photophase seems to exist, when the females deposited 67.8% of the eggs.

Longevity

Males lived significantly longer than females (t-test, $P < 0.05$). The mean longevity of males was 49.3 ± 26.4 days and that of females was 33.7 ± 14.1 days. As shown in Fig. 2, the maximum longevity observed was 114 days for the males and 79 days for the females. The 50% level of mortality was observed when the males were 45 days old and the females 33 days old.

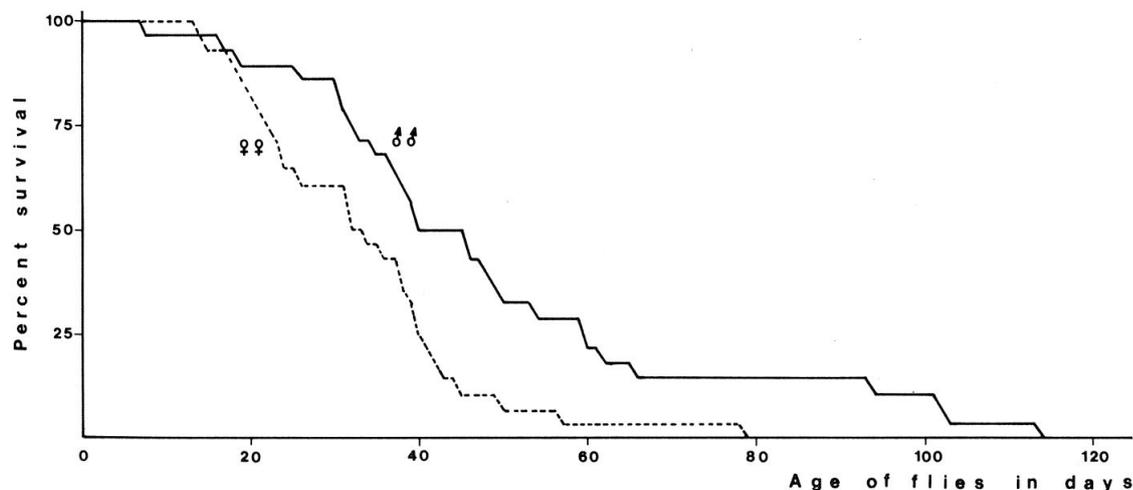


Fig. 2. Longevity of *C. australis* flies under laboratory conditions (28 males, 28 females held as pairs, with YST buds).

Preoviposition period

Under laboratory conditions (25 °C) the shortest preoviposition period was two days (Fig. 3). As soon as the third day after emergence, about 30% of the mated females and about 10% of the virgin females began to lay their eggs. Most of the mated females (about 85%) had already oviposited on the 6th day and the maximum (94.7%) on the 18th day, whereas the maximum of virgin females (55.5%) had oviposited on the 19th day.

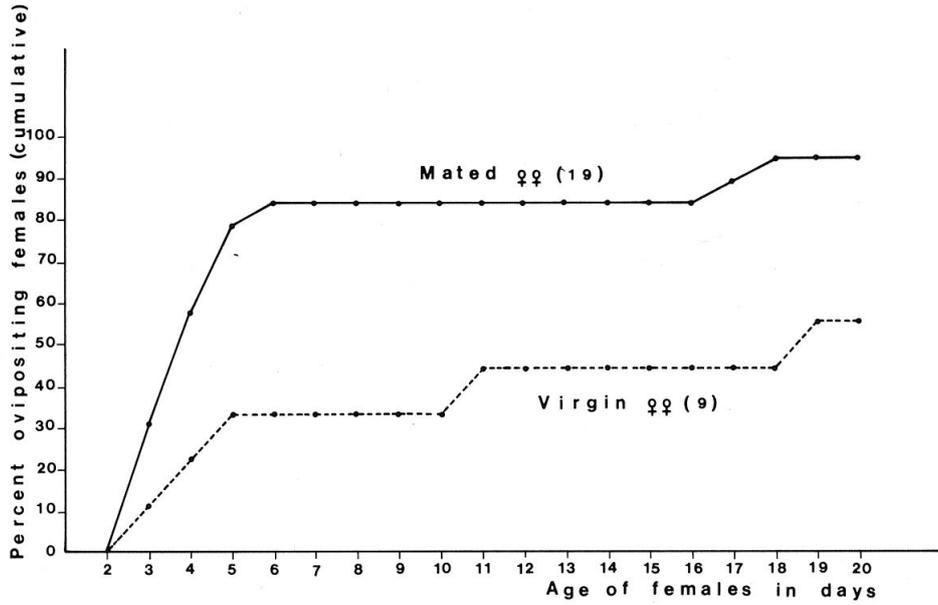


Fig. 3. Cumulative percentage of individually caged, ovipositing *C. australis* females in the laboratory, at 25° C (N = 19 mated, 9 virgin females).

Influence of age and mating on fecundity and fertility

The mean number of eggs deposited by ovipositing mated females was 79.1 ± 66.9 (N = 18), whereas the mean number for ovipositing virgin females was 20.8 (N = 5). The means for all females, ovipositing or not, were 74.9 ± 67.6 (N = 19) and 11.6 (N = 9) respectively. The maximum number of eggs deposited by a female throughout its life was 242 eggs for the mated and 68 for the virgin females.

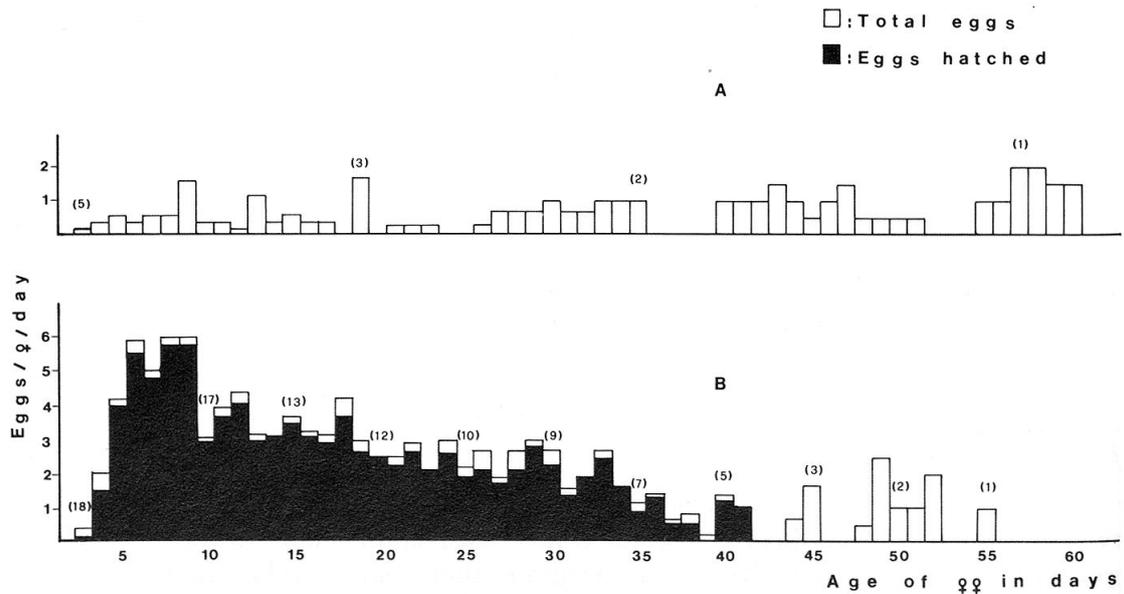


Fig. 4. Average daily oviposition and egg hatchability of caged *C. australis* females. A: one virgin female per cage (N = 9), B: one pair per cage (N = 19). Calculations of means for each day were based on ovipositing only females. The number of surviving females are given in brackets.

Most of the mated ovipositing females (68.4%) deposited 1 to 100 eggs, whereas fewer females (26.3%) deposited 101 to 242 eggs. The percentage of mated females which did not oviposit was very low (5.3%). By contrast, the percentage of virgins which did not oviposit was high (44.4%) and most of the ovipositing virgin females laid 1 to 50 eggs. The percentage of egg hatchability was very high for eggs deposited by mated females (90.5% out of 1423 eggs), whereas none of the 104 eggs laid by virgin female hatched.

The number of eggs laid per ovipositing female and day, as well as the number of hatched eggs is given in Fig. 4. As shown, the number of eggs per mated female and the hatchability were low on the first and second oviposition day, then the number of eggs increased and after the 9th day it began to decline. Fertile eggs were deposited until the 41st day. The few females which oviposited after the 41st day laid almost all their eggs directly on the bud surface instead of under the bracts, and these eggs shrivelled and did not hatch. Only a few virgin females laid during their entire life a limited number of unfertile eggs.

The maximum number of eggs deposited by a female in one day was 17 (mated, on the 9th day) and 8 (virgin, on the 9th day). The last surviving female oviposited on its 55th day after emergence and the last surviving virgin on its 60th day.

The differences in egg production between virgin and mated females clearly show that mating, similar to other tephritids (cf. KATSOYANNOS *et al.*, 1987), has a strong effect not only on the fertility but also on the fecundity of *C. australis*. This needs to be further investigated. Our results on longevity, fecundity and fertility confirm and complete the preliminary observations reported by SOBHIAN & ZWÖLFER (1987) and SOBHIAN & PITTARA (1988).

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ZUSAMMENFASSUNG

Das Eiablageverhalten von *Chaetorellia australis* HERING (Diptera, Tephritidae) Weibchen, die im Labor mit ihren natürlichen Eiablagesubstraten wie Blütenknospen von *Centaurea solstitialis* L. und *Centaurea cyanus* L. (Asteraceae, Cardueae) gehalten wurden, wird beschrieben, sowie Laborstudien über die Lebensdauer, Fekundität und Fertilität dieser Fliege. Bei 25°C betrug die durchschnittliche Lebensdauer bei Männchen 49,3 Tage und die der Weibchen 33,7. Die kürzeste beobachtete Präovipositionsperiode war 2 Tage, und 85% der begatteten Weibchen begannen am 6. Tag nach dem Schlüpfen mit der Eiablage. Diese fand während der ganzen Photophase statt, und die Eiablageperiode dauerte 50 Tage. Während ihres Lebens legten begattete Weibchen durchschnittlich 74,9 Eier (Maximum 242), von denen 90,5% fertil waren. Unbegattete Weibchen legten durchschnittlich 11,6 unfertile Eier.

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