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Research Article

Temperature dependent development of the egg-larval parasitoid *Chelonus oculator* on the factitious host, *Ephestia cautella*

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Abstract: Development, fecundity, and longevity of the egg-larval parasitoid *Chelonus oculator* Panzer (Hymenoptera: Braconidae) were studied on the factitious host, *Ephestia cautella* (Walker) (Lepidoptera: Pyralidae) at 4 different temperatures (15 °C, 20 °C, 25 °C, and 30 °C). Developmental time from egg to adult was inversely related to temperature. Egg to adult development time ranged from 188 days at 15 °C to 28 days at 30 °C. Complete development required 489 degree-days with a developmental threshold of 12.5 °C. Adult male and female longevity ranged from 43 days at 20 °C to 17 days at 30 °C. Maximum production of offspring per female (2626 ± 152) was obtained at 25 °C. Sex ratios were female-biased at 15 °C (0.8♂:1♀), but were increasingly male-biased at higher temperatures to a maximum of 4.4♂:1♀ at 30 °C. The highest net reproductive rate was 168.7 at 25 °C, whereas the highest intrinsic rate of increase and the shortest doubling time occurred at 30 °C.

Key words: *Chelonus oculator*, development, egg-larval parasitoid, *Ephestia cautella*, temperature

Yumurta-larva parazitoiti *Chelonus oculator*'un laboratuvar konukçusu *Ephestia cautella* üzerinde sıcaklığa bağlı gelişimi

Özet: Bu çalışmada yumurta-larva parazitoiti *Chelonus oculator* Panzer (Hymenoptera: Braconidae)'un laboratuvar üretim konukçusu *Ephestia* cautella (Walker) (Lepidoptera: Pyralidae) üzerinde 4 farklı sıcaklıkta (15 °C, 20 °C, 25 °C ve 30 °C) gelişme süresi, meydana gelen birey sayısı ve ömür uzunluğu belirlenmiştir. Parazitoitin yumurtadan ergine kadar gelişme süresi sıcaklık artışı ile ters bir orantı göstermiş; 15 °C'de 188 günde gelişmişken, 30 °C'de gelişimini 28 günde tamamlamıştır. Parazitoitin gelişme eşiği 12.5 °C, termal konstantı ise 489.3 gün-derece olarak bulunmuştur. Ergin erkek ve dişi ömür uzunluğu 20°C'de 43 gün iken 30 °C'de 17 gün olmuştur. Dişi başına meydana gelen birey sayısı en fazla (2626 ± 152) 25 °C'de görülmüştür. Artan sıcaklık cinsiyet oranını erkekler lehine değiştirmiş, 15 °C de 0.8♂ : 1♀ olan cinsiyet oranı 30 °C de 4.4♂ : 1♀'e yükselmiştir. En yüksek net üreme oranı (R_0) 25 °C de (168.7 adet) gerçekleşmiştir. En yüksek doğal artış kapasitesi ve popülasyonun ikiye katlandığı en düşük süre 30 °C'de gözlenmiştir.

Anahtar sözcükler: *Chelonus oculator*, gelişim, *Ephestia cautella*, sıcaklık, yumurta-larva parazitoiti

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Introduction

Chelonus oculator Panzer (Hymenoptera: Braconidae) is an arrhenotokous, solitary, egg-larval parasitoid (Ozkan and Ozmen 2001, Ozmen et al. 2002) of several important lepidopterous pests occurring throughout the Caucasus, Kazakhstan, Central Asia, North Africa, Iran, and Western Europe (Tobias 1995). Male progeny of the parasitoid develops parthenogenetically from unfertilized (haploids) and fertilized (diploids) eggs while female progeny develops from only fertilized (diploids) eggs. Females lay single eggs in the eggs of the host species. The first and second-instar larval parasitoids feed inside the developing host. The third–instar larva exits the host to feed externally, eventually consuming the entire host except for the exoskeleton and head capsule. The parasitoid then spins its cocoon within the host's pupal cell. Parasitized host larvae have reduced feeding, which further increases the value of *C. oculator* as a biocontrol agent. Reported hosts include *Agrotis segetum* Denis & Schiffermüller, *Helicoverpa armigera* Hübner, *Heliothis viriplaca* Hufnagel, *H. peltigera* Denis & Schiffermüller, *Spodoptera exigua* Hübner, *Photedes 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). Consequently, *C. oculator* is of interest as a potential biocontrol agent.

Laboratory studies showed that *C. oculator* could be reared on factitious hosts, *Ephestia kuehniella* Zeller (Ozkan and Ozmen 2001, Ozkan et al. 2005, Ozkan 2006), and *Ephestia* (=*Cadra*) *cautella* (Walker) and *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) (Ozkan and Tunca 2005, Ozkan 2005). However, all these studies were conducted only at 25 °C. The objective of this study was to investigate the effect of temperature on the development, reproduction, and longevity of *C. oculator* on *E. cautella*. This information is necessary to determine the potential effectiveness of the parasitoid as a biological control agent.

Materials and methods

Biology of *Chelonus oculator*

E. cautella and *C. oculator* were reared according to the methods described by Ozkan and Tunca (2005). Laboratory experiments were performed at different temperatures (15 °C, 20 °C, 25 °C, and 30 °C), 60%-70% R.H., and 16:8 h (L:D) photoperiod. In the experiment, 15, 7, 10, and 13 pairs of newly (<3 h) emerged adult *C. oculator* were used for 15 °C, 20 °C, 25 °C, and 30 °C, respectively. Each pair of adults was placed in glass vials (3 × 17 cm). The open end of the vial was enclosed with gauze in order to hold the parasitoids. Pure honey was provided daily by smearing a small amount on the lid of the vials. The parasitoids were allowed to mate for 24 h before host eggs were supplied. Approximately 400 eggs (24- to 48-h-old) were stuck on a paper sheet (0.8 × 10 cm) with the help of 5% solution of gum arabic and introduced into each vial. Females were allowed to forage and oviposit for 24 h. The adult parasitoids were then transferred into another vial with 400 eggs for another 24 h. This procedure was repeated every 24 h until the death of female parasitoids. Parasitized eggs were transferred into a clear plastic container (20 × 15 × 7.5 cm) containing approximately 250 g sterilized diet consisting of a 2:1:0.25:0.50:0.25:0.25 mixture of wheat bran, corn flour, dry yeast, honey, milk powder, and glycerin. Adult wasp eclosion was checked at regular intervals of 12 h, which enabled development times to be accurately recorded. Life history traits, namely adult longevity, fecundity, oviposition period, post-oviposition period, and sex ratio of the progeny, were recorded. In addition, developmental threshold and thermal constant were defined.

Data analysis

Data on development time, longevity, fecundity, oviposition and post-oviposition time, and sex ratio were analyzed through one-way analysis of variance (PROC ANOVA, SAS Institute 2003) and significant differences ($P < 0.05$) were identified using the Duncan's test. The life table parameters, namely intrinsic rate of increase (r_m), net reproductive rate (R_o), mean generation time (T), doubling time (DT), and finite rate of increase (λ), were computed according to Birch (1948) using a statistical jackknife technique (Maia et al. 2000). The life table parameters were compared using one-way ANOVA and means were separated using the Duncan's test at a significant level of $\alpha = 0.05$ (SAS Institute 2003). Degree–days needed for development was calculated as: $DD = (T - T_0) \times D$, where T is treatment temperature (°C), T_0 is lower developmental threshold temperature, and D is the mean development time in days at temperature T.

Results

Developmental period

The development time of the parasitoid decreased as temperature increased ($F = 220.0$, $P < 0.001$) (Table 1). The developmental time from egg to adult ranged from 188.8 days at 15 °C to 27.9 days at 30 °C. Similarly, the longest and the shortest developmental periods were observed at 15 °C and 30 °C for male ($F = 200.0$, $P < 0.001$) and female parasitoids, respectively ($F = 70.0$, $P < 0.001$) (Table 1). The minimum development threshold for total development time was 12.5 °C and the calculated thermal constant (K) for *C. oculator* was 489 degree-days above the threshold.

Longevity, reproduction of adult females, and sex ratio

Temperature affected total longevity of *C. oculator* ($F = 102.0$, $P < 0.001$). The mean longevity decreased with increased temperature from 20 °C (43.0 days) to 30 °C (17.1 days) except at 15 °C (26.8 days). Similar results were obtained for male ($F = 52.9$, $P < 0.001$) and female longevities ($F = 49.2$, $P < 0.001$). Maximum longevity for male (44.2 days) and female (41.7 days) adults occurred at 20 °C. Minimum longevity for male (18.2 days) and female (16.1 days) adults occurred at 30 °C.

The average number of offsprings was affected by temperature ($F = 108.4$, $P < 0.001$) (Table 2). The average number of offsprings produced by individual wasps over their lifetime was highest (2625.9) at 25 °C and lowest (5.3) at 15 °C. For *C. oculator*, the average daily fecundity of offspring produced per female ranged from 0-30, 1-1434, 13-1287 and 13-1318 at 15 °C, 20 °C, 25 °C, and 30 °C, respectively. Survival curves of the female parasitoids differed between temperatures (Figure 1).

Similarly, temperature significantly affected the oviposition and post-oviposition period of the females (Table 2). The oviposition period of *C. oculator* ranged from 2.4 days at 15 °C to 31.6 days at 25 °C ($F = 98.8$, $P < 0.001$). The post-oviposition period decreased depending on the temperature and ranged from 16.5

Table 1.The average development time of *Chelonus oculator* reared on *Ephestia cautella* at 4 constant temperatures.

Temperature (°C)	Development time of *Chelonus oculator* (d)		
	♂	♀	♂+♀
15	188.5 ± 0.27 a (187-194) n = 36	189 ± 0.30 a (187-197) n = 44	188.8 ± 0.21 A (187-197) n = 80
20	64.9 ± 0.06 b (52-96) n = 7765	65.8 ± 0.08 b (53-99) n = 3492	65.2 ± 0.05 B (52-99) n = 11257
25	43 ± 0.02 c (37-54) n = 19509	44 ± 0.04 c (38-77) n=6747	43.2 ± 0.01 C (37-77) n = 26256
30	27.8 ± 0.02 d (21-41) n = 11076	28.4 ± 0.05 d (22-42) n = 2703	27.9 ± 0.02 D (21-42) n = 13779

Within the same column, the values with different letters are significantly different at $P < 0.05$
n: sample size,
( ): minimum and maximum values
±: means followed by standard error

Table 2. The average longevity, fecundity, oviposition, post-oviposition periods, and sex ratio of *Chelonus oculator* at 4 constant temperatures.

Temperature (°C)	Female longevity (days)	Lifetime fecundity (♀/♀)	Oviposition period (days)	Post-oviposition period (days)	Sex ratio ♂:♀
15	26.2 ± 0.61 c (23-31) n = 15	5.3 ± 1.06 d (0-13) n = 15	2.4 ± 0.43 c (0-5) n = 15	16.5 ± 2.72a (0-27) n = 15	0.81:1d
20	41.7 ± 1.23 a (36-45) n = 7	1608.1 ± 143.39 b (887-1937) n = 7	28.7 ± 1.41 a (23-35) n = 7	12 ± 1.78a (8-20) n = 7	2.28:1c
25	34.7 ± 2.49 b (19-43) n = 10	2625.9 ± 152.37 a (1608-3155) n = 10	31.6 ± 2.20 a (17-40) n = 10	2.1 ± 0.52b (0-5) n = 10	2.89:1b
30	16 ± 1.41 d (9-23) n = 13	1059.9 ± 125.48 c (357-1719) n = 13	14.6 ± 1.41 b (7-21) n = 13	0.5 ± 0.18b (0-3) n = 13	4.35:1a

Within the same column, the values with different letters are significantly different at $P < 0.05$
n: sample size
( ): min and max value
±: means followed by standard error

days (15 °C) to 0.5 days (30 °C) ($F = 18.1$, $P < 0.001$) (Table 2).

Temperature also affected sex ratio ($F = 114.4$, $P < 0.001$) (Table 2). Increasing temperatures caused male biased sex ratio, and the ratio 0.81:1 (♂ : ♀) at 15 °C increased to 4.4:1 (♂ : ♀) at 30 °C.

Life table parameters

The effect of temperature on net reproduction rate (R_o), intrinsic rate of increase (r_m), finite rate of increase (λ), mean generation time (T), and doubling time (DT) are shown in Table 3. Mean generation time decreased with increasing temperatures from 192 days at 15 °C to 37.1 days at 30 °C. Net reproduction peaked at 25 °C (168.7 viable females per female), and doubling time decreased from 279.4 days to 7 days across the temperature range of 15 °C to 30 °C. Both the finite rate of increase and the intrinsic rate of increase reached their respective maximums at 30 °C. The intrinsic rates of increase at 25 °C and 30 °C were significantly higher than they were at 15 °C and 20 °C ($F = 1497.6$, $P < 0.001$).

Discussion

The results indicated that the development time of the parasitoid significantly decreased with increasing temperature and shorter duration was observed at 30 °C (Table 1). Several researchers have already reported that *Chelonus* species have different development times depending on host species and temperature ranges. Rechav and Orion (1975) observed that *C. inanitus* (L.) developed in 36.2 days at 28 °C, and 32.1 days at 32 °C on *E. cautella*. They also noted that the parasitoid developed on *E. kuehniella* in 88, 61.6, 54.5, and 51.4 days at 20 °C, 25 °C, 28 °C, and 32 °C, respectively. *C. blackburni* (Cameron) completed its development in 31.5 days on *Pectinophora gossypiella* (Saunders) (Lepidoptera: Gelechiidae) at 25 °C (Jackson et al. 1978), 25.8 days on *Phthorimaea operculella* (Zeller), and 42.5 days on *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae) at 24 °C (Kumar and Ballal 1990). Male and female of *C. oculator* developed in 55.9 days and 58.6 days, respectively, at 25 °C on *E. kuehniella* (Ozkan and Ozmen 2001).

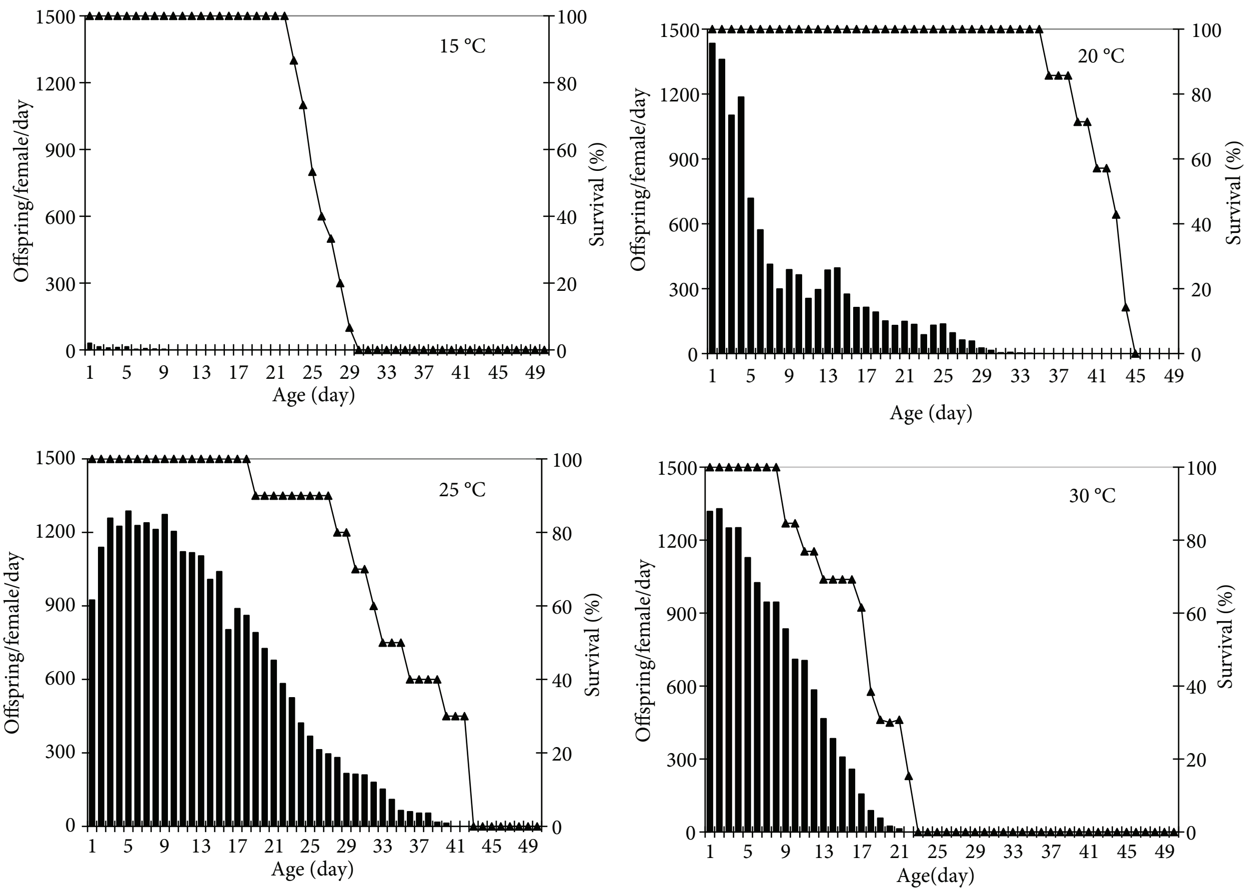

Figure 1. Age-specific fecundity bars and age-specific survival lines for female Chelonus oculator at 4 constant temperatures.

Table 3. Life table parameters for *Chelonus oculator* at 4 constant temperatures.

Parameter	Temperature (°C)			
	15	20	25	30
Net reproduction rate (R_0) (female progeny/female)	1.6	154.6	168.7	39.5
Intrinsic rate of increase (r_m) * (female/female/day)	0.0024 ± 0.0002 b	0.0721 ± 0.0004 c	0.0936 ± 0.001 a	0.0990 ± 0.002 a
Finite rate of increase (λ) (female/female/day)	1.00	1.07	1.09	1.10
Mean generation time (T) (days)	192	69.8	54.7	37.1
Doubling time (DT) (days)	279.4	9.6	7.3	7

*The same letter after standard error in row indicate no significant difference at $P < 0.05$

The results showed that longevity of *C. oculator* at 15 °C and 30 °C was shorter than at 20 °C and 25 °C. Negative effects at both high and low temperatures on insects have been reported by some other researchers (Hutchinson et al. 1986; Mendel et al. 1987). According to Jervis and Kidd (1996), parasitoids are more resistant to lower and higher temperatures than their host, but like their host, parasitoids cannot tolerate lower and higher temperatures for extended periods and as a result of thermal stress, death may occur. Several researchers already reported that *Chelonus* species have various longevities at different temperatures. The average longevity of *C. curvimaculatus* (Cameron) was 11.4 days at 26.5 °C (Broodrky 1969). On average, males and females of *C. heliopae* (Gupta) lived for 4.8 and 6.3 days at 26.7 °C (Patel and Patel 1971). Females and males of *C. formosanus* (Sonan) lived for 10.3 days and 5.0 days at 26.7 °C, respectively (Rao and Patel 1974). The average longevities of *C. inanitus* (L.) females were reported as 39.5, 33.2, and 19.4 days at 10 °C, 15 °C, and 20 °C, respectively (Kolaib et al. 1987). Decreasing longevity was also reported for *C. sp. nr. curvimaculatus* (Cameron) and females lived 16.5 and 12 days at 20 °C and 25 °C, respectively. The longevity of *C. blackburni* (Cameron) females ranged from 14-22 days at 25 °C (Rangadhamaiah et al. 1984).

The parasitoid produced an average of 2626 progenies per female at 25 °C, which was the highest rate of all *Chelonus* species from several reported reports. It seems that temperature is an important factor for the fecundity of *C. oculator* (Table 2). Ozkan et al. (2005) indicated that *C. oculator* produced an average of 2344 progenies per female at 25 °C on *E. kuehniella*. The realized fecundity of C. *curvimaculatus* (Cameron) was 522 at 26.5 °C (Broodryk 1969). Patel and Patel (1971) found that average egg laying potential of *C. heliopae* (Gupta) was 1178 eggs per female. Rao and Patel (1974) showed the differences between egg laying potential and realized fecundity on *C. formosanus* (Sonan); the average egg laying potential of parasitoid was 697 eggs, whereas the average realized fecundity was 299 individuals. The realized fecundity of *C. inanitus* (L.) was also higher (1219 progenies) at 28 °C (Rechav 1978a). *C.* sp. nr. *curvimaculatus* (Cameron) produced potentially 1034 eggs but realized fecundity was only 420 eggs at 25 °C (Hentz et al. 1998).

The observation showed that the female parasitoid was able to parasitize immediately after eclosion. Previous studies showed that the pre-oviposition period in pro-ovigenic *C. oculator* was less than 24 h (Ozkan and Ozmen 2001). In Hymenoptera (Flanders 1950), species fall into either of 2 categories; pro-ovigenic or synovigenic. Pro-ovigenic insects complete oogenesis either before or very soon after eclosion. The results indicated that the oviposition period of *C. oculator* increased at higher temperatures up to 30 °C and as temperature increased post-oviposition periods decreased accordingly (Table 2). Rao and Patel (1974) found that pre-oviposition and oviposition periods of *C. formosanus* (Sonan) were 3.7 and 6.6 days at 26.7 °C, respectively.

The results indicated that *C. oculator* offspring was mostly male-biased, except at 15 °C (Table 2). Kfir and Luck (1979) reported that female ratio of *Aphytis melinus* (DeBach) and *A. lingnanensis* (Compere) (Hymenoptera: Aphelenidae) decreased as temperature increased. A similar result was revealed by Rechav (1978b) for *C. inanitus* (L.). Like other *Chelonus* species, *C. oculator* is a parthenogenetic braconid, and thus unmated females produced males only and mated females produced both males and females. In arrhenotokously reproducing parasitoids skewed sex ratio is common place (Hamilton 1967; Luck et al. 1993).

The highest net reproductive value was observed at 25 °C; however, the highest rate of increase was observed at 30 °C. That may be explained by the shorter generation time observed at 30 °C. In addition to this, the doubling time was shortest at 30 °C because of the fact that the highest rate of population increase (r and λ) and the shortest generation time occurred at 30 °C. Ozkan et al. (2005) showed that the net reproduction rate, the mean generation time and the intrinsic rate of increase for *C. oculator* on *Ephestia kuehniella* at 25 °C was 111 female/ female, 64.4 days and 0.0723 female/female/day, respectively. Hentz et al. (1998) indicated that the net reproduction rate for *C. sp. nr. curvimaculatus* on *Pectinophora gossypiella* was 118.3 at 25 °C and 62.6 at 30 °C.

R_o, λ, r_m, T, and DT values indicate that *C. oculator* is relatively sensitive to changes in temperature. The data would be of great value for maintaining the culture of *C. oculator* in laboratory conditions and in accordance with the need; the emergence of the parasitoid might be delayed by regulating the rearing temperature. The results regarding the effect of temperature may provide a basis for understanding the interactions between the parasitoid and changing temperatures. Findings presented here may also contribute to the development of an effective mass rearing strategy for *C. oculator* using the factitious host *E. cautella* for biological control of the lepidopteran pests.

Acknowledgments

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