

Oviposition Model of *Trissolcus basalis* Wholaston (Hym.: Scelionidae) on Sunn Pest Eggs

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ABSTRACT

Longevity, survivorship, and fecundity of *Trissolcus basalis* Wholaston were studied on sunn pest eggs at 17.5, 20, 25, 27, 30 and 35°C (all ± 0.5), 60 $\pm 5\%$ RH and 16:8 h L:D. The preliminary results revealed an effect of temperature on the mentioned traits. In general, longevity decreased as temperature increased and ranged from 53.28 ± 5.9 to 10.68 ± 1.13 days when temperature leveled up from 17.5 to 35°C. Similarly, the highest and lowest fecundity was observed at 25 and 35°C (292.40 ± 11.14 and 42.16 ± 8.62 eggs female⁻¹), respectively. Moreover, the developmental rate of adult parasitoids (1/median longevity) was well described by modified model of Sharp-DeMichele in the range of studied temperatures and it was used to calculate physiological age. Likewise, the relationship between temperature and total realized fecundity was fitted well to a quadratic polynomial function. Conspicuously, age-specific cumulative fecundity rate was highly coordinated with exponential model and adult survivorship was fitted well to the reversed logistic curve. Finally, three temperature-dependent attributes *viz.*, total fecundity, age-specific cumulative fecundity rate, and age-specific survivorship rate were used for *T. basalis* oviposition modeling. These findings may contribute to better understanding of oviposition strategy and behavior of *T. basalis*.

Keywords: Oviposition model, Physiological age, Survival, Temperature, *Trissolcus basalis*.

INTRODUCTION

Although *Trissolcus basalis* Wolaston is considered as one of the most important parasitoids of sunn pest eggs in Iran (Amir-Maafi, 2010; Radjabi and Amir-Nazari, 1988), the only available information on the wasp is its geographical distribution. However, global literature review shows that there are a number of studies conducted on different aspects of *T. basalis* biology on *Nezara viridula* eggs. For instance, *T. basalis* biology and life table parameters on *N. viridula* eggs (Porta and La Porta, 1992), geographical population characteristics of the wasp (Awan *et al.*, 1990), reproductive

capacity (Correa-Ferreira and Zamataro, 1989), optimum temperature determination (25°C) (Powell *et al.*, 1981; Correa-Ferreira and Moscardi, 1994; Awadalla, 1996; Jones and Westcot, 2002), mating behaviour of *T. basalis* (Loch and Walter, 1999, 2002), mating behavior and host acceptance (Sales *et al.*, 1978; Colazza *et al.*, 1996; Weber *et al.*, 1996) and effect of temperature and host age on the *T. basalis* growth and development (Awadalla, 1996) are mentioned.

Similarly, Sales (1979) demonstrated a very important relationship between number of host eggs and foraging female *T. basalis*. He proved that the ovipositing threshold was

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5 host eggs for 12 hours per female. Moreover, it is known that the size of egg masses visiting by the wasp would affect sex ratio and oviposition sequence (Colazza and Wajnberg, 1998; Colazza *et al.*, 1991). In a study on the inter and intra-specific interaction of green sting bug parasitoids, it was shown that *T. basalis* was a very aggressive species, therefore, this issue should be considered while releasing the parasitoid with regard to its host range (Sujii *et al.*, 2002).

Among abiotic factors, temperature has a very significant effect on regulating insects' physiological system. Thereby, in pest bicontrol, estimation of development rate, longevity, survivorship, fecundity and thermal threshold of both pest and natural enemy has received great attention not only for a better understanding of their population dynamics but also in development of IPM (Huffaker *et al.*, 1999).

Therefore, the present study was taken up to determine the influence of temperature on oviposition of *T. basalis* and to develop its oviposition model. The model may be applied in parasitism prediction and developing population dynamics trend of *T. basalis*.

MATERIALS AND METHODS

Parasitoid Rearing

Wild population of *T. basalis* was collected from wheat fields in Varamin, Iran, and maintained at $16\pm 1^\circ\text{C}$, $60\pm 5\%$ RH and 16:8 h L:D in $20\times 13\times 7$ cm Plexiglas boxes for about 7 months (Amir-Maafi, 2000; Shahrokhi, 1997). Then, they were reared on sunn pest eggs at $25\pm 1^\circ\text{C}$ and the mentioned humidity and daylight for one generation. Afterwards, 150 F_2 mated female parasitoids 0-4 hour old were selected randomly from the main colony and each 25 females were confined in Plexiglas boxes separately and assigned randomly to either of six incubator set up at predefined temperatures (17.5 ± 0.5 , 20 ± 0.5 , 25 ± 0.5 ,

27.5 ± 0.5 , 30 ± 0.5 and $35\pm 0.5^\circ\text{C}$ and all at $60\pm 5\%$ RH and 16:8 h L:D). Daily, two masses of sunn pest eggs (~28) were presented per female parasitoid in each rearing box until their death and parasitized eggs were removed and reared at similar conditions of related treatment, separately. Biological parameters such as longevity, adult daily survivorship, fecundity (number of parasitized eggs) and offspring numbers and sexes were recorded for each female.

Data Analysis

The data collected on the effect of temperature on longevity and fecundity was analyzed through GLM procedure (SAS, ver. 9.1) considering unbalanced variances. Data transformation was conducted prior to any analysis. The means were grouped based on Tukey test (SAS, ver. 9.1). Sigmaplot (ver. 12) and Excel software were used to plot figures.

Oviposition Strategy Modeling

Adult Female Physiological Age

Developmental rate of adult parasitoids or inverse of median longevity (1/median longevity in days) was used as a function of temperature for modeling through modified Equation (1) of Sharp-DeMichele (Schoolfiel *et al.*, 1981):

$$r(T) = \frac{\rho_{(25^\circ\text{C})} \frac{T}{298} \exp\left[\frac{\Delta H_A}{R} \left(\frac{1}{298} - \frac{1}{T}\right)\right]}{1 + \exp\left[\frac{\Delta H_L}{R} \left(\frac{1}{T_{1/2L}} - \frac{1}{T}\right)\right] + \exp\left[\frac{\Delta H_H}{R} \left(\frac{1}{T_{1/2H}} - \frac{1}{T}\right)\right]} \quad (1)$$

Where, $r(T)$ is the developmental rate at temperature $T(^{\circ}\text{K})$, R represents the universal gas constant ($1.987\text{cal degree}^{-1} \text{mol}^{-1}$), $\rho_{(25^\circ\text{C})}$ denotes the developmental rate at 25°C (298.15°K) assuming no enzyme activity at the mentioned temperature and ΔH_A , ΔH_L , $T_{1/2L}$, ΔH_H and $T_{1/2H}$ are the parameters

depicting kinetics of the rate-controlling enzymes. Parameters were estimated using SAS NLIN Proc (SAS ver. 9.1) based on the algorithm rendered by Wagner *et al.* (1984). The model was employed to calculate the physiological age of *T. basalis* female parasitoid. The physiological age of adult females (P_x) since their eclosion to n^{th} day is defined as follow (Curry and Feldman, 1987):

$$P_x = \int_0^n r(T_i) \approx \sum_{i=0}^n r(T_i) \quad (2)$$

Where, $r(T_i)$ is the development rate of adult female at $T(^{\circ}\text{K})$ since i^{th} day after their eclosion.

Temperature Dependent Fecundity Model

The mean of total eggs laid (mean fecundity) is equal to total eggs laid by all females divided by total number of females used in the test. The relationship between mean fecundity and temperature ($^{\circ}\text{C}$ degree) was confirmed using quadratic polynomial function [Equation (3)] through Table Curve software (Jandel Scientific, 1996):

$$f(T_c) = a + bT_c + cT_c^2 \quad (3)$$

Where, $f(T_c)$ is total eggs laid by each female during its life time at temperature T_c ($^{\circ}\text{C}$ degree) and a , b , and c are the model coefficients.

The Age-specific Cumulative Egg Laying Model

An exponential equation was employed to model the age specific cumulative egg laying:

$$p(P_x) = \frac{1}{1 + e^{(\alpha + \beta P_x)}} \quad (4)$$

Where, $p(P_x)$ is the rate of cumulative eggs laid by each adult female at physiological age (P_x) and α and β are constant coefficients. The relative rate of mean number of egg laid at each age is obtained via mean rates of cumulative egg laid. After physiological age calculation [Equation (2)], the relationship between

mean rate of cumulative egg laid and physiological age was analyzed using non-linear regression. Then, parameters of age-specific egg laying curve model was estimated by Proc NLIN (SAS, ver 9.1).

Age-specific Survival Rate Model

A sigmoid function was applied to describe age-specific survival distribution of female *T. basalis*. Then, the survival proportion at physiological age P_x was fitted to the following equation [Equation (5)]:

$$s(P_x) = \frac{1}{1 + e^{(\gamma - P_x)/\delta}} \quad (5)$$

Where, $s(P_x)$ is the proportion of live females at physiological age P_x , γ is the physiological age at which the survivorship would be equal to 50% and δ is a constant coefficient. The parameters were predicted by Proc NLIN (SAS, ver 9.1).

Daily Egg Production

Cumulative eggs laid by each female parasitoid at i^{th} day e.g physiological age P_{xi} , was calculated by multiplying total temperature-dependent eggs [$f(T_c)$], age-specific egg laying rate [$p(P_{xi})$] and age-specific survival rate [$s(P_{xi})$]. Therefore, the number of eggs laid during P_{xi} and P_{xi+1} physiological age intervals can be obtained by the following Formula (6):

$$\text{Noeggslaid}(P_{xi} \sim P_{xi+1}) = f(T_c) [p(P_{xi+1}) - p(P_{xi})] \frac{s(P_{xi}) + s(P_{xi+1})}{2} \quad (6)$$

RESULTS

Longevity and Fecundity

It was found that temperature had significant effects on *T. basalis* longevity and fecundity ($F = 21.56$, $df = 5, 144$, $P <$



0.0001). As Table 1 shows, in general, longevity decreased with an increase in temperature and was the longest (53.28 ± 5.9 days) at 17.5°C . However, it decreased to 10.68 days at 35°C . The developmental rate of female *T. basalis* (1/median longevity) was fitted well to the modified model of Sharp-DeMichele model in the range of 17.5 to 35°C (Table 2, Figure 1).

Moreover, despite significant effect of the tested temperatures ($F = 39.73$, $df = 5, 144$, $P < 0.0001$) on the fecundity, *T. basalis* females laid eggs at all the tested temperatures. The maximum and minimum fecundities (292.40 ± 11.14 and 42.16 ± 8.62 eggs) were observed at 25 and 35°C , respectively. However, fecundity (number of laid eggs) was not significantly different at 17.5 , 20 , and 27°C (Table 2).

Oviposition Model

The relationship between total eggs laid and temperature was highly described by a binomial model (Figure 2-a, Table 3), through which the maximum fecundity would be predicted. Figure 2-b shows cumulative age specific fecundity rate. Changes in cumulative egg production at different temperatures decreased conspicuously with physiological age decrement and were fitted well to a power model (Table 3, Figure 2-b). As it is obvious in Figure 2-b, 50% of eggs were laid at 0.2 physiological age.

The relation between survivorship and physiological age was demonstrated well with sigmoid function (Figure 2-c, Table 3). The survivorship showed that mortality was

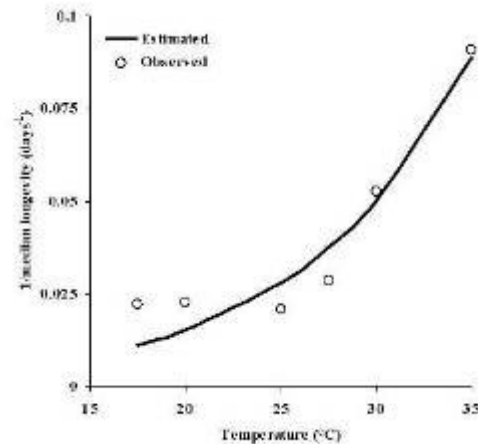


Figure 1. Adult developmental rate curve (1/median longevity) of female *Trissolcus basalis*. A four parameter poikilothermal model of Schoolfield et al. (1981) was applied with low temperature inhibition.

sporadic at the beginning of physiological age; afterwards, it increased linearly in the middle, but again levelled off at the ultimate points of physiological age. Indeed, 50% of mortality occurred at 0.85 physiological age (Figure 2-c). Moreover, Figure 3 shows that no eggs were laid below 10°C , but, as temperature increased, egg deposition started slowly. The lower part of egg laying curve (between 10 - 20°C) is somewhat plateau and the maximum fecundity at this thermal range is 15 eggs female⁻¹ day⁻¹ (Figure 3). However, at the higher temperatures ($> 20^\circ\text{C}$) the length of oviposition duration decreases drastically and fecundity reaches its maximum value with a sharp slope during early days after adult emergence (33 eggs female⁻¹ day⁻¹ at 32.5°C). Finally, egg laying stops at above 35°C (Figure 3).

Table 1. Female adult longevity and total number of eggs laid per female of *Trissolcus basalis* at different constant temperatures.

Temperature ($^\circ\text{C}$)	No. adult examined	Longevity in days (Mean \pm SE)	Total eggs female ⁻¹ (Mean \pm SE)
17.5	25	53.28 ± 5.9 a	253 ± 19.94 ab
20	25	49.48 ± 5.44 a	248.24 ± 15.47 ab
25	25	43.16 ± 2.05 ab	292.40 ± 11.14 a
27.5	25	32.42 ± 1.39 cb	251.44 ± 10.15 ab
30	25	21.44 ± 2.36 cd	196.80 ± 16.49 b
35	25	10.68 ± 1.13 d	42.16 ± 8.62 c

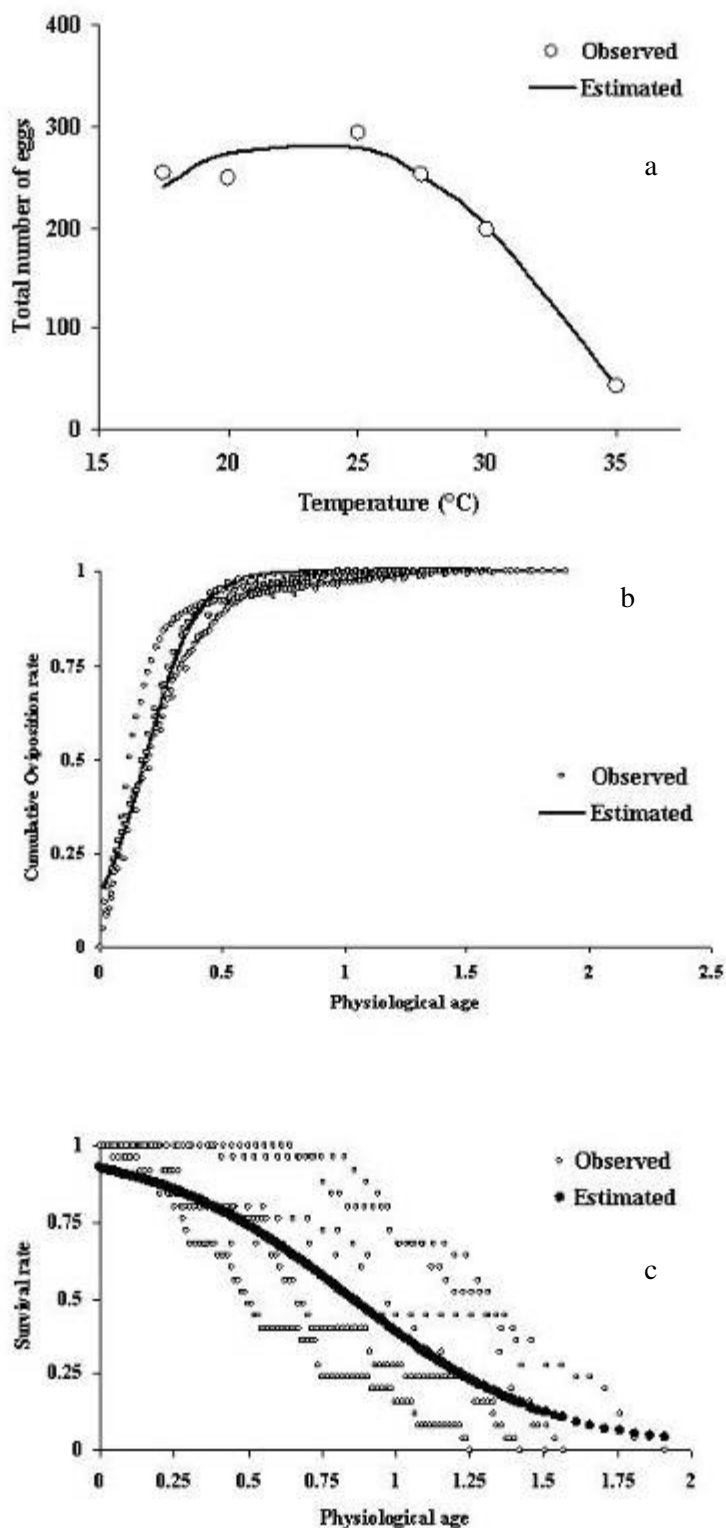


Figure 2. Major components of oviposition model of *Trissolcus basalis*. (a) Temperature-dependent total fecundity curve; (b) Age-specific cumulative oviposition rate curve; (c) Age-specific survival rate curve.



Table 2. Estimated values of parameters for adult developmental rate curve (1/median longevity) of female *Trissolcus basalis*.

Parameters	Estimated values	S.E.M	r^2
$\rho_{(25^\circ)}$	0.02797	0.0037	
ΔH_A	47.9264	5.88	0.92
ΔH_L	18373.928	4100.519	
$T_{1/2L}$	700.6343	41.326	

Table 3. Estimated values of parameters for oviposition model components of *Trissolcus basalis*.

Models	Parameters	Estimated Values	S.E.M	r^2
Temperature-dependent fecundity model	total a	-566.8	154.91	0.98
	b	74.74	12.325	
	c	-1.638	0.236	
Age-specific cumulative oviposition rate model	α	1.7834	0.0542	0.99
	β	-9.7218	0.2445	
Age-specific survival rate model	γ	0.8523	0.0181	0.92
	δ	-0.3362	0.0193	

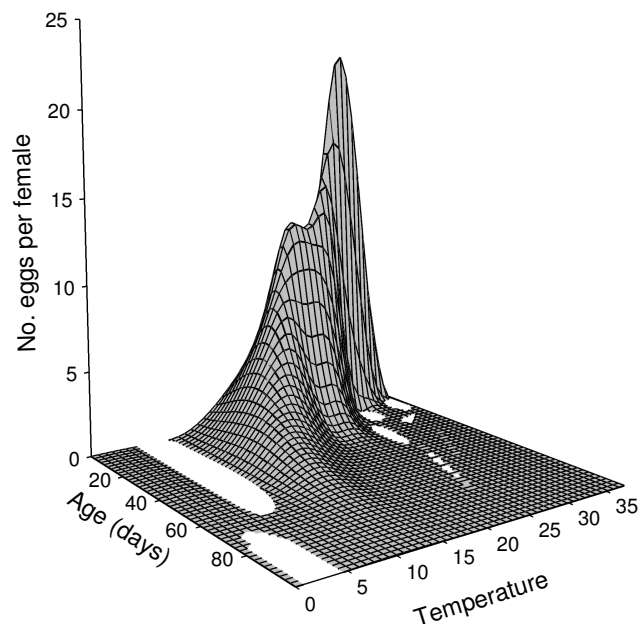


Figure 3. Predicted oviposition density curves of *Trissolcus basalis* in relation to cohort age and temperature.

DISCUSSION

Despite the important role of *T. basalis* in Iran's cereal plantations (Amir-Maafi, 2010; Radjabi and Amir-Nazari, 1988), not much information is available on its biological attributes. We obtained a series of biological characters which may explain the pivotal role of *T. basalis* in biological control programmes of sunn pest. Primarily, it should be noticed that Boivin (2010) discussed several proxies such as fecundity, longevity, mating ability etc, based on which the fitness of a parasitoid could be estimated. He also believed that when the parasitoid phenotype was modified by a temperature at which an individual developed, the resulting phenotype would vary based on the life history strategy of the parasitoid. Besides, there is a lot of information available on the fitness consequences of reproductive behavior of parasitoids on host-parasitoid interaction, which in turn affects their population dynamics (Godfray, 1994). Having said that, Mack and Smith (1992) believe any factor that directly or indirectly affects an insect may modify its oviposition.

Result obtained here on the relationship between temperature and fecundity pattern of *T. basalis* is similar to those of closely related species reported by Amir-Maafi (2010). He proved that the maximum number of eggs by *T. grandis*, *T. vasilievi* and *T. semistriatus* was obtained at 25-32°C and the oviposition activity out of this range would decrease. Therefore, the oviposition model rendered here would properly describe reproductive activity of *T. basalis*. Awan *et al.* (1990) found that the egg laying pattern of three different populations of *T. basalis* on *N. viridula* eggs was maximum in the first week of oviposition at normal temperatures, which is in accordance with our findings. Iranipour *et al.* (2010) reported the effect of temperature on biological attributes of two *T. grandis* populations. Amazingly, in one population the maximum fecundity was observed at lowest tested temperature (~117 eggs female⁻¹ at 20°C), which is in contrast with what we found on fecundity of *T. basalis* in the present study (~292 at 25°C). Kivan and Kilic (2006) studied developmental rate of *T. rufiventris* and *T. simoni* and observed that by increasing temperature from 20 to 32°C, the developmental

rate speeded up greatly and from 20-24 days declined to 6-9 days, respectively, which agrees with some of our findings. Similarly, reproduction and survival of overwintered and F1 generation of two egg parasitoids of sunn pest showed somewhat common responses to temperature (Tarla and Kornosor, 2009). Recent studies on temperature-dependent development modeling on other insect groups have also been done (Damos and Savopoulous-Soultani, 2008; Pakyari *et al.*, 2012; Jalali *et al.*, 2010; Seo and Kim, 2012).

As Pakyari *et al.* (2012) have expressed, in many random phenological models for arthropods, a calendar time or degree-day is used as time scale. In the case of degree-day based models, in addition to minimum and maximum temperatures, the assumption of linear relationship of development rate and temperature should be adopted. Based on such conditions and assumption, Howe (1967) concluded that the required temperature during a normal growth would be less for temperatures close to lower threshold and very high for the temperatures around upper threshold. However, the presented model for *T. basalis* used here holds on physiological age based on the summation of developmental rate and has been applied by Shaffer and Gold (1985), Wagner *et al.* (1984), Berry *et al.* (1991), Kim and Lee (2003), Pakyari *et al.* (2012), and Kim (2009). In some other investigations a phenological and reproductive model by direct incorporation of temperature and using calendar time as age variable has been introduced (Afen *et al.*, 1995).

Many researchers have revealed the temperature as the main factor influencing insects' fecundity (Goodenough *et al.*, 1983; Harrison *et al.*, 1985; Hansen and Jensen, 2002). However, there are other abiotic factors such as light intensity (Wyatt and Brown, 1977) and biotic agents like food (host) (Leather and Dixon, 1982; Kaakeh and Dutcher, 1993) which may have an impact on their fecundity. Although it has been reported that host species and humidity would strongly impinge on egg laying behavior of *T. basalis* (Forouzan *et al.*, 2013), in this research, only three thermal dependent components (total fecundity, age specific egg laying rate, and age specific survivorship rate) were incorporated into the model. The equations were selected based on their potential goodness



of fit, but the parameter values were estimated by real data obtained through laboratory investigations.

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مدل تخم‌ریزی زنبور (*Trissolcus basalis* (Hym: Scelionidae) روی تخم سن گندم

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چکیده

طول عمر، بقاء و باروری زنبور پارازیتوئید *Trissolcus basalis* Wholaston روی تخم سن گندم در دماهای ۱۷/۵، ۲۰، ۲۵، ۲۷/۵، ۳۰ و ۳۵ (±۰/۵) درجه سلسیوس، رطوبت نسبی ۶۰±۵ درصد و دوره روشنایی ۱۶ و تاریکی ۸ ساعت مطالعه شد. نتایج اولیه حاکی از تاثیر دما روی صفات مورد بررسی بود. به طور کلی، طول عمر با افزایش دما از ۱۷/۵ به ۳۵ درجه سلسیوس به ترتیب از ۵۳/۲۸±۵/۹ روز به ۱۰/۶۸±۱/۱۳ روز کاهش یافت. به همین ترتیب، بیشترین و کمترین میزان باروری در ۲۵ و ۳۵ درجه سلسیوس (به ترتیب ۱۱/۱۴±۱۱/۴۰ و ۴۲/۱۶±۸/۶۲ تخم / ماده) مشاهده شد. بعلاوه، نرخ رشد حشرات بالغ (۱/ میانه طول عمر) به خوبی با مدل تغییر یافته شارپ و دومیشل در دامنه دماهای مورد مطالعه توصیف گردید و از آن برای محاسبه سن فیزیولوژیک استفاده شد. در ادامه، رابطه بین دما و تعداد کل تخم گذاشته شده به خوبی با تابع چند جمله‌ای درجه دوم توصیف شد. نرخ تخم گذاری تجمعی ویژه-سنی به وضوح با مدل نمایی انطباق یافت و بقا حشرات بالغ نیز به خوبی با منحنی لجستیک معکوس توصیف شد. در نهایت، از سه جزء وابسته به دما شامل باروری کل، نرخ تخم گذاری ویژه-سنی و نرخ بقاء ویژه-سنی برای مدل سازی تخم گذاری استفاده شد. این یافته‌ها می‌تواند به درک بهتر استراتژی و رفتار تخم گذاری زنبور پارازیتوئید *T. basalis* کمک کند.