



Temperature-dependent parasitism model of *Trissolcus grandis* Thompson (Hymenoptera: Scelionidae)

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Abstract. *Trissolcus grandis* Thompson (Hymenoptera: Scelionidae), a native Sunn pest egg parasitoid in Iran, has the potential as a biological control agent for sunn pest, *Eurygaster integriceps* Puton (Het.: Scutelleridae). However, its ecological characteristics have remained unclear. Thus, this study aimed to develop a parasitism model of *T. grandis* with sunn pest egg as host. In order to obtain the data for the model, the longevity, survivorship and parasitism capacity of the adult female *T. grandis* were examined at nine constant temperatures (15, 17.5, 20, 25, 27.5, 30, 32.5, 35, and 37.5 ± 0.5 °C), relative humidity 65 ± 5% RH, and a photoperiod of 16:8 (L:D) h. Longevity (mean±SE) decreased as temperature increased and was the longest at 15°C (73.18 ± 3.86 days) and the shortest at 35°C (18.98 ± 0.48 days). A modified model of Sharp-DeMichele well described adult developmental rate (1/mean longevity) in the range of studied temperatures ($r^2 = 0.994$) and was used to calculate the physiological age. The mean total host eggs parasitized/female (mean ± SE) was greatest at 17.5°C (275.84 ± 3.21 host eggs) and lowest at 15°C (25.06 ± 3.221 host eggs). The temperature-dependent total parasitism, the age-specific cumulative parasitism rate, and the age-specific survival rate were best described by an extreme value function ($r^2 = 0.934$), the two-parameter Weibull function ($r^2 = 0.967$), and a sigmoid function ($r^2 = 0.979$), respectively. I anticipate that the fitted models and parameters may be useful in developing a population model for *T. grandis* and lead to a better understanding of its parasitism strategy.

Keywords: Biological control, Egg parasitoid, parasitism, survival, parasitism model, temperature

Article History

Received:

7 October 2022

Accepted:

13 February 2023

Subject Editor:

Ahad Sahragard

Citation: Amir-Maafi, M. (2023) Temperature-dependent parasitism model of *Trissolcus grandis* Thompson (Hymenoptera: Scelionidae). *J. Entomol. Soc. Iran* 43 (2), 87-96.

Introduction

Sunn pest, *Eurygaster integriceps* Puton (Hem.: Scutelleridae), is a serious pest of wheat and barley throughout West and Central Asia (Critchely, 1998; Davari & Parker, 2018). Insecticides are commonly applied to prevent pest economic damage at a large scale. A recent survey demonstrates that approximately two million ha of cereals are sprayed by chemical pesticides against Sunn pests annually (Anonymous, 2022). Nevertheless, the massive use of chemicals increases production costs and usually results in the reduction of beneficial insects and pest resurgence, and leads to other environmental problems. Among alternative control methods, biological control agents are potentially very useful in wheat integrated pest management programs (Amir-Maafi, 2000; Amir-Maafi *et al.*, 2002; Amir-Maafi & Parker, 2002, 2003).

Egg parasitoids (Scelionidae) are important natural enemies of sunn pests. Much of the initial studies on sunn pest egg parasitoids were done in Iran (Alexandrov, 1947; Safavi, 1968; Rakhshani *et al.*, 2008; Minab *et al.*, 2023) and Morocco (Delucchi, 1961), and attempts were made to introduce some species from North Africa to the former USSR (Shapiro *et al.*, 1975). However, these early attempts were barely enough to achieve

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successful biological control. A wide range of sunn pest egg parasitoids has been recorded, mostly belonging to the family Scelionidae (including *Trissolcus* and *Telenomus* species) and some to the Encyrtidae and Eupelmidae families (Rosca *et al.*, 1996). In Iran, complexes of the pest egg parasitoid species appear to vary, depending on region and habitat, but the dominant species in this complex is *T. grandis* (Amir-Maafi, 2000; Amir-Maafi & Parker, 2002, 2003). Thereby, some studies have been conducted on the biology and rearing methods of *T. grandis* (Safavi, 1968; Shapiro *et al.*, 1975, Gusev & Shmettser, 1977; Taghadosi, 1991; Shahrokhi, 1997; Amir-Maafi, 2000; Shirazi, 2006; Amir-Maafi & Parker, 2011).

In recent years in Iran, there has been an emphasis on the chemical control of overwintered Sunn pest population, concurring with its egg parasitoids, especially *T. grandis*. Thus, the prediction of parasitism and its occurrence is important for the timing of control actions, especially during the early season, since egg parasitoids are the most vulnerable to insecticides. Therefore, an understanding of the Sunn pest egg parasitoids' oviposition is essential for the prediction of the parasitoids' occurrence and in explaining the parasitism pattern in fields. In the simplest approach, a population model of *T. grandis* could be used for the timing of chemical control (conservation of this parasitoid) and to enhance the prediction of its performance. Because the fecundity of solitary parasitoids is equal to its potential, we can use the Curry & Feldman (1987) method to express parasitism. Therefore, parasitism can be described by three temperature-dependent components: total parasitism (total fecundity of parasitoids), age-specific parasitism rate (ovipositional rate of parasitoids), and age-specific survival rate.

Since few studies have been conducted on *T. grandis* under a limited range of temperatures (Taghadosi, 1991; Amir-Maafi, 2000; Amir-Maafi & Parker, 2011; Nozad Bonab *et al.*, 2014), sufficient quantitative information is not yet available for the development of a parasitism model. Therefore, the objectives of this study were to determine the effects of temperature on *T. grandis* parasitism and to develop a parasitism model for *T. grandis*, which can be used in predicting parasitism occurrence and in developing a *T. grandis* population dynamics model.

Materials and methods

Insect colonies

Sunn pest parasitized egg masses were collected from wheat and barley fields in Varamin, Iran, from April to May 2021. Emerged wasps were identified and, adults of *T. grandis* were stored in a growth chamber (Model: Phytotron 600-Ax, Noorsanat Azma Ferdous Company, Karaj, Iran) at 16 ± 1 °C, 65 ± 5 %RH, and 16:8 (L:D) in $20 \times 14 \times 7$ cm polystyrene boxes for about 8 months. Meanwhile, wasps were provided with food and water once a month (Amir-Maafi, 2000). Then, they were reared on Sunn pest eggs at 25 ± 1 °C, 65 ± 5 %RH, and 16:8 (L:D) photoperiod for one generation. Afterward, newly-emerged adult parasitoids (F2) were used for the oviposition experiment. One newly-emerged female (<4 h-old) was placed with one male wasp (<4 h-old) in an oviposition polystyrene cage ($14 \text{ cm} \times 7 \text{ cm} \times 4 \text{ cm}$). Two masses (28 eggs) of sunn pest eggs were placed in a cage for oviposition, and honey was provided as food. The oviposition cages were maintained at constant temperatures in incubators at 15, 17.5, 20, 25, 27.5, 30, 32.5, 35, and 37.5 °C (± 0.5), 65 ± 5 %RH, and a photoperiod of 16:8 (L:D) h. At each temperature, 50 female *T. grandis* were examined. Males that died during the early ages of their life spans were replaced with new males to ensure mating. Two host egg masses were replaced with two new egg masses every day. The number of surviving female adults (longevity) and the number of parasitized host eggs were recorded daily until female adult death.

Data analysis

The effect of temperature on longevity and number of host eggs parasitized by *T. grandis* (parasitism, hereafter) were analyzed using the PROC GLM module of SAS (ver. 9.4), and means were separated using Tukey's studentized range test at $P=0.05$ when analysis of variance showed significant difference (SAS Institute 2019).

Parasitism model component

Adult development

The relationship between the adult developmental rate (the reciprocal of mean adult longevity) and the temperature was described by the modified Sharpe and DeMichele model (Schoolfeld *et al.*, 1981) because it is based on accepted biophysical laws and has parameters that can be interpreted biologically (Wagner *et al.* 1984). This model is:

$$r(T) = \frac{\rho_{25} \times (T/298.15)^{\times} \times e^{[(H_A/R) \times (1/298.15 - 1/T)]}}{1 + e^{[(H_L/R) \times (1/T_L - 1/T)]} + e^{[(H_H/R) \times (1/T_H - 1/T)]}} \quad (1)$$

where $r(T)$ is developmental rate at temperature T ($^{\circ}K$), R represents the universal gas constant (1.987 cal/degree/mol), ρ_{25} denotes developmental rate at $25^{\circ}C$ (298.15 $^{\circ}K$) assuming no enzyme inactivation, and H_A , T_L , H_L , T_H , and H_H represent the parameters of kinetics of the rate-controlling enzymes. Parameters were estimated using the SAS program based on Wagner *et al.* (1984).

The development model was utilized for calculating the physiological age of *T. grandis* adults. The physiological age (Px) of adults from the starting time to the n th time step was defined as below (Curry & Feldman 1987):

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

where $r(Ti)$ is the development rate at temperature T ($^{\circ}K$) of i th time step (e.g., day).

Temperature-dependent total parasitism function

Mean total parasitism by *T. grandis* was calculated by dividing the sum of total host eggs parasitized by all adults by the number of adults examined. An extreme value function (Kim & Lee, 2003a) was used to describe the relationship between total parasitism and temperature:

$$f(Tc) = ae^{[1 + ((b - Tc)/k) - e^{((b - Tc)/k)}]} \quad (3)$$

where $f(Tc)$ is the number of total host eggs parasitized by a female at temperature T ($^{\circ}C$), a is the maximum parasitism capacity, b is the temperature ($^{\circ}C$) at which maximum parasitism occurs, and k is a fitted constant.

Age-specific cumulative parasitism rate function

The age-specific cumulative parasitism rate is the proportion of the total lifetime parasitism potential that elapses during each time. It was fitted using the two-parameter Weibull model:

$$p(Px) = 1 - e^{-(Px/\alpha)^{\beta}} \quad (4)$$

where $p(Px)$ is the cumulative proportion of host eggs parasitized by physiological age Px by a female adult, and a and b are fitted as constants.

Age-specific survival rate

A sigmoid function was used to describe the age-specific survival distribution of *T. grandis* females. The survival proportions at physiological age (Px) were fitted by this function:

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

where $s(Px)$ is the proportion of live females at the physiological age Px , γ is the physiological age at 50% survival, and δ is the parameter defining steepness of this equation.

The parameters of all equations were estimated using PROC NLIN in SAS ver. 9.4 (SAS Institute 2019).

Host egg parasitism

Eventually, the number of host eggs parasitized by a female *T. grandis* during the physiological age interval between Px_i and Px_{i+1} can be calculated as:

$$f(Tc)[p(Px_{i+1}) - p(Px_i)] \frac{s(Px_i) + s(Px_{i+1})}{2} \quad (6)$$

Results

Temperature-dependent longevity and total parasitism

The longevity and total host egg parasitized (total parasitism) by adult female *T. grandis* were significantly influenced by temperature (Table 1) (longevity: $F_{8, 441} = 59.76$, $p < 0.0001$; total parasitism: $F_{8, 441} = 89.98$, $p < 0.0001$). The longevity of females decreased as temperature increased and was the longest at 15 °C (73.18 days), however, it was as short as 18.98 days at 35 °C. Examining total parasitism at all temperatures revealed that fewer host eggs were significantly parasitized at 15 and 32.5–37.5 °C. Host egg parasitism was the highest at temperatures between 17.5–30 °C and then declined steadily thereafter.

Parasitism model

Adult development function

The adult developmental rate (1/mean longevity) was well described by the nonlinear biophysical developmental model [($F_{4,5} = 202.25$, $P < 0.0001$), (poikilotherm rate model, Schoolfield *et al.*, 1981), (Table 2, Fig. 1)]. The high temperature threshold of female was 38.24°C.

The relationship between total parasitism and temperature has been well described by the extreme value function (equation 3; Fig. 3a). In the model, the estimated maximum parasitism was 287.3 host eggs per female (parameter *a*) at 27.5 °C (Table 3).

The age-specific cumulative parasitism rate curve was well fitted to Eq. (4). The variations of cumulative parasitism among different temperatures were reduced using physiological age scale, and are well described by the two-parameter Weibull function (Fig. 2b, Table 3). In the model, fifty percent of the total host eggs were parasitized by ≈ 0.13 physiological age.

Female survival curves normalized using the physiological age were well described by the sigmoid function (Eq. 5). Death of female adults started to occur at 0.01 physiological age after emergence, while 50% of adults survived until ≈ 0.85 physiological age (Fig. 2c, Table 3).

The regression models for the components of the parasitism model were statistically significant for each equation (Total parasitism: $F_{3, 6} = 28.15$, $p = 0.0006$; Parasitism rate: $F_{2, 543} = 8038.41$, $p < 0.0001$; Survival rate: $F_{2, 543} = 12482.6$, $p < 0.0001$). The predicted parasitism density curve indicating the relationship between female age and temperature showed a higher and wider shape in the 17.5–30 °C range. However; the parasitism and parasitism period decreased at lower and higher temperatures (Fig. 3).

Table 1. Adult longevity and total number of host eggs parasitized by female *T. grandis* at different constant temperatures

Temperature (°C)	No. adults examined	Longevity in days (mean \pm S.E.M)	Total host eggs parasitized/female (mean \pm S.E.M)
15	50	73.18 \pm 3.86a	25.06 \pm 3.221e
17.5	50	61.38 \pm 5.23b	275.84 \pm 19.96a
20	50	54.9 \pm 2.89b	207.94 \pm 10.75b
25	50	28.42 \pm 2.13cd	242.68 \pm 9.25ab
27.5	50	32.5 \pm 1.25c	245.34 \pm 4.54ab
30	50	27.38 \pm 1.71cd	192.96 \pm 12.28bc
32.5	50	20.92 \pm 0.32e	77.24 \pm 8.52d
35	50	18.98 \pm 0.45e	64.42 \pm 6.85de
37.5	50	20.60 \pm 1.21e	54.86 \pm 6.896de

Means followed by the same letter within a column are not significantly different ($P > 0.05$, Tukey studentized range test)

Table 2. Estimated parameter values for adult developmental rate curve (1/mean longevity) of *Trissolcus grandis*.

Parameters	Estimated values	S.E.M	r^2
RHO25	0.027	0.001	0.994
HA	11298.9	1808.3	
HH	209290	30061.2	
TH	311.4	0.911	

The predicted parasitism density curve indicating the relationship between female age and temperature showed a higher and wider shape in the 17.5–30 °C range. However; the parasitism and parasitism period decreased at lower and higher temperatures (Fig. 3). Moreover, the lower part of the parasitism curve (between 10–17.5 °C) is somewhat plateau and the maximum parasitism at this thermal range is 25 host eggs. However, in the range of 17.5–30 °C, the length of oviposition duration decreases drastically and parasitism reaches its maximum value with a sharp slope during the early days after adult emergence. Finally, at temperatures higher than 30 °C, the peak of parasitism and parasitism period sharply decreased.

Discussion

Trissolcus grandis is an important parasitoid of sunn pest eggs in Iran and has shown considerable ability to regulate Sunn pest populations (Amir-Maafi, 2000; Amir-Maafi & Parker, 2002, 2003). Thus, studying ecology, especially the parasitism pattern, of *T. grandis* would be valuable for establishing a biological control program. The literature contains scarce information on the effect of temperature on the parasitism capability of *T. grandis*, and only a few studies have examined the reproductive biology of *T. grandis* (Taghadosi, 1991; Amir-Maafi, 2000; Amir-Maafi & Parker, 2011; Nozad Bonab *et al.*, 2014). There are a few differences in published reproductive biology. Such differences can be intrinsically present in populations of various origins.

This is the first study to report *T. grandis* parasitism at a wide range of temperatures and enabled us to develop a parasitism model for *T. grandis*. For this reason, and because the fecundity of solitary parasitoids is equal to its potential, I used the Curry & Feldman (1987) method to express parasitism, an approach that has been applied to construct an oviposition model for many arthropod pests (Kim & Lee, 2003a; Kim & Lee, 2003b; Marchioro & Foerster, 2012; Pakyari *et al.*, 2012; Kim *et al.*, 2013; Kang *et al.*, 2015; Pakyari *et al.*, 2016; San Choi & Kim, 2016; Baek *et al.*, 2017; Lee *et al.*, 2018; Noor-ul-Ane *et al.*, 2018; Choi *et al.*, 2020; Farazmand & Amir-Maafi, 2020; Park & Lee, 2020; Geng *et al.*, 2021; Noor-ul-Ane & Jung, 2022).

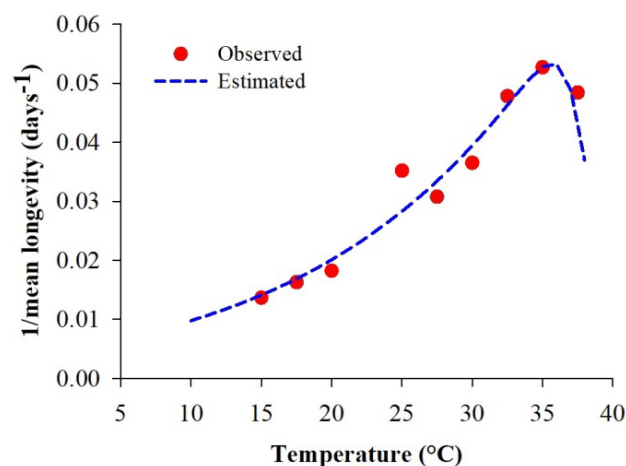


Fig. 1. Adult developmental rate curve (1/mean longevity) of female *Trissolcus grandis*. Four-parameter poikilothermic model of Schoolfield *et al.* (1981) was applied with high temperature inhibition.

Table 3. Estimated parameter values for parasitism model components of *Trissolcus grandis*.

Models	Parameters	Estimated values	S.E.M	r^2
Temperature-dependent Total parasitism model	a	287.3	44.369	0.934
	b	22.258	0.829	
	k	5.825	1.035	
Age-specific cumulative parasitism rate model	α	0.208	0.011	0.967
	β	0.689	0.037	
Age-specific survival rate model	γ	1.002	0.007	0.979
	δ	-0.283	0.007	

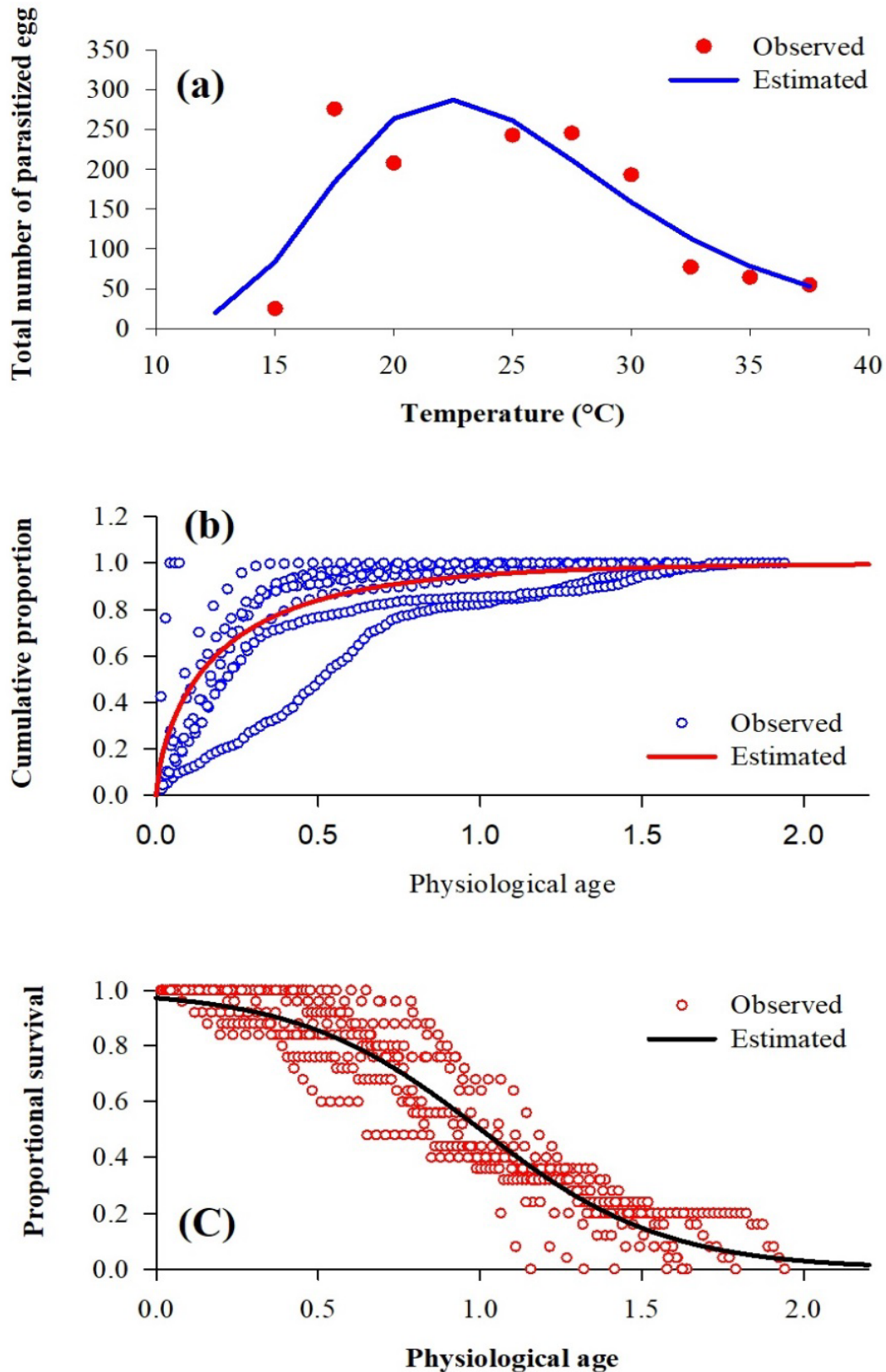


Fig. 2. Major components of parasitism model of *Trissolcus grandis* (a) Temperature-dependent total parasitism curve; (b) age-specific cumulative parasitism rate curve; (c) age-specific survival rate curve.

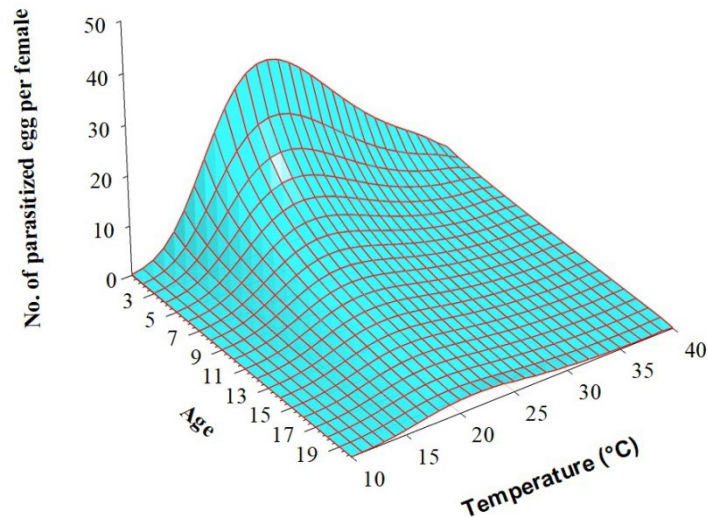


Fig. 3. Predicted parasitism density curves of *Trissolcus grandis* in relation to cohort age and temperature.

In the present study, *T. grandis* can develop its population at least at temperatures from 15 to 37.5 °C and showed interesting biological traits at different temperatures. Minimum parasitism was observed at the extreme temperature (i.e. lower than 17.5°C and higher than 30 °C). On the contrary, Forouzan *et al.*, (2015) showed that the longevity and fecundity of adult *T. basalis* were greater at mid-temperatures (20-30°C). The *T. grandis* wide temperature-adapting ecological characteristic may explain why it is abundant in wheat and barley fields during spring and especially early in the season. The results obtained here on the relationship between temperature and parasitism pattern of *T. grandis* are similar to those reported by Amir-Maafi (2000) and the field study conducted by Amir-Maafi & Parker (2002, 2003) on the seasonal abundance of sunn pest egg parasitoids.

Thereby, three basic components were provided to develop the parasitism model of *T. grandis* using experimental laboratory data sets: temperature-dependent total parasitism, the age-specific cumulative parasitism rate, and the age-specific survival rate model.

It is highly advantageous that the biological details of *T. grandis* parasitism were incorporated into the model; therefore, it might be able to provide a better understanding of *T. grandis* parasitism phenology in the field and to improve the previous model developed by Amir-Maafi (2000).

Acknowledgments

I thank Homa Pourhosseini and Asieh Abolhassani for their technical assistance.

Funding

This research was supported by a grant from Iranian Research Institute of Plant Protection, Iran, project No. 2-16-16-089-000898.

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مدل پارازیتیسیم وابسته به دما *Trissolcus grandis* Thompson (Hymenoptera: Scelionidae)

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تاریخچه مقاله

دریافت: ۱۴۰۱/۰۷/۰۹ | پذیرش: ۱۴۰۱/۱۱/۲۴ | دبیر تخصصی: احد صحراگرد

چکیده

زنبور *Trissolcus grandis* پارازیتویید بومی تخم سن گندم در ایران بوده و با اینکه به‌عنوان عامل کنترل بیولوژیک سن گندم *Eurygaster integriceps* است، اما ویژگی‌های اکولوژیک آن کاملاً روشن نشده است. بنابراین هدف این مطالعه، توسعه مدل پارازیتیسیم *T. grandis* بر روی تخم میزبان آن بود. برای دستیابی به داده‌های لازم برای این مدل، طول عمر و بقاء حشرات ماده *T. grandis* و ظرفیت پارازیتیسیم آن در ۹ دما (۱۵، ۱۷/۵، ۲۰، ۲۵، ۲۷/۵، ۳۰، ۳۲/۵، ۳۵ و $۳۷/۵ \pm ۰/۵$ درجه سلسیوس)، رطوبت ۶۵ ± ۵ درصد و طول دوره روشنایی ۱۶ ساعت و تاریکی ۸ ساعت مطالعه شد. طول عمر (میانگین \pm خطای معیار) با افزایش دما کاهش یافت و بلندترین طول عمر در دمای ۱۵ درجه سلسیوس ($۳/۸۶ \pm ۳/۱۸$ روز) و کوتاه‌ترین در دمای ۳۵ درجه سلسیوس ($۰/۴۸ \pm ۱۸/۹۸$ روز) بود. نرخ رشد حشرات بالغ (۱/ میانگین طول عمر) بخوبی با مدل تغییر یافته شارپ-دومیشل در دامنه دمای مورد مطالعه برازش یافت ($r^2 = ۰/۹۹۴$) و از آن برای محاسبه سن فیزیولوژیک استفاده شد. میانگین تعداد کل تخم‌های میزبان پارازیتیه شده به ازای هر ماده (میانگین \pm خطای معیار) در دمای ۱۷/۵ درجه سلسیوس بیشترین ($۳/۲۱ \pm ۲۷۵/۸۴$ تخم میزبان) و در دمای ۱۵ درجه سلسیوس کمترین ($۳/۲۲۱ \pm ۲۵/۰۶$ تخم میزبان) میزان را داشت. پارازیتیسیم کل وابسته به دما با تابع extreme value برازش یافت ($r^2 = ۰/۹۳۴$). نرخ پارازیتیسیم تجمعی ویژه سنی بخوبی با تابع دوپارامتری میبول توصیف شد ($r^2 = ۰/۹۶۷$). نرخ بقاء ویژه سنی نیز بخوبی با مدل سیگموئیدی برازش یافت ($r^2 = ۰/۹۷۹$). انتظار می‌رود که مدل‌های برازش یافته و پارامترهای آن‌ها برای توسعه مدل جمعیتی *T. grandis* و درک بهتر از استراتژی پارازیتیسیم آن مفید باشند.

کلمات کلیدی: کنترل بیولوژیک، پارازیتویید تخم، پارازیتیسیم، بقاء، مدل پارازیتیسیم، دما

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Citation: Amir-Maafi, M. (2023) Temperature-dependent parasitism model of *Trissolcus grandis* Thompson (Hymenoptera: Scelionidae). *J. Entomol. Soc. Iran* 43 (2), 87-96. <https://doi.org/10.61186/jesi.43.2.1>