Modeling temperature-dependent development of *Trissolcus grandis* Thomson (Hymenoptera: Scelionidae)

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Abstract. *Trissolcus grandis* Thomson, is an important egg parasitoid of *Eurygaster integriceps* Puton that can control its population in wheat and barley fields. Despite valuable results from previous studies, the thermal development of *T. grandis* over a wide range of temperatures had not been elucidated completely. This study was conducted to evaluate the thermal effect on the development of *T. grandis* using Sunn pest eggs as hosts in a wide range of temperatures (12.5 to 40 ±0.5°C, 65 ± 5% RH., and a photoperiod of 16L:8D h) in the laboratory condition. The development times of the immature stage (Egg-Adult) of *T. grandis* decreased with increasing temperatures up to 35 °C for both sexes. Patterns of temperature-dependent development times of the immature stage of females and males (i.e. emergence of females and males of *T. grandis* adults) were modeled and simulated with linear and nonlinear regression analyses. The estimated low-threshold temperatures (*T*<sub>L</sub>) were 10.61 and 10.62 °C for females and males, respectively. Thermal constants (*k*) of the immature stage of females and males were 179.85 and 161.03 degree-days (*DD*), respectively. Stage transition models for females and males adults of *T. grandis* were constructed using two basic components of nonlinear development rate (modified Sharpe & DeMichele model function) and distribution models (two-parameter Weibull function) to simulate the proportion of individuals shifted from egg to adult. These models will be useful in building a *T. grandis* population model that will describe its seasonal occurrence pattern and population dynamics under various wheat and barley fields and optimize environmental conditions in mass rearing.

Keywords: *Trissolcus grandis*, egg parasitoid, Sunn pest, developmental rate, stage emergence model

Introduction

As is well known, Sunn pest, *Eurygaster integriceps* Puton (Hem.: Scutelleridae), is a serious pest of wheat and barley in IRAN and nearby countries in Eastern Europe, Southern CIS, and Near and Middle East (Miller & Morse, 1996). In these regions, chemical control is the most usual control method (Critchley, 1998). In IRAN, about 2 million ha of wheat must be sprayed with pesticides yearly to control this insect (Anonymous, 2023), with the growing environmental hazards caused by the conventional use of insecticides. An integrated management program is developed for Sunn pest, the utilization of a complex of hymenopteran egg parasitoids (Amir-Maafi, 2000). Egg parasitoids (Scelionidae) are important natural enemies of Sunn pest. Much of the initial studies on Sunn pest egg parasitoids were done in IRAN (Alexandrov 1948a, b; Safavi, 1968) and Morocco (Deluchi, 1961), and attempts were made to introduce several species from North Africa into the USSR (Shapiro et al., 1975). However, these early attempts to achieve biological control were never successful. Complex of parasitoid species depending on region and habitat appears to vary. However, four species of *Trissolcus* (*Trissolcus grandis* Thomson, *T. vassilievi* Mayr, *T. semisteriatus* Nees and *T. basalis* Wollaston) were reported as an important egg parasitoids, of *E. integriceps* (Amir-Maafi, 2000; Amir-Maafi & Parker, 2002, 2003). The dominant species in this complex is *Trissolcus grandis* Thomson (Hymenoptera: Scelionidae) (Alexandrov 1948a, b; Safavi, 1968, 1970; Shushanov, 1955, 1957; Gourieva, 1957; Deluchi, 1961; Safavi & Badii, 1964; Safavi & Eshaghi, 1968). The biological control of Sunn pest was studied by T. Thomson (Hymenoptera: Scelionidae) (T. Thomson, 1864). This species is known as an important egg parasitoid of *E. integriceps* Puton (Hem.: Scutelleridae). The egg parasitoids (Scelionidae) are important natural enemies of Sunn pest. The biological control of Sunn pest was studied by T. Thomson (Hymenoptera: Scelionidae) (T. Thomson, 1864). This species is known as an important egg parasitoid of *E. integriceps* Puton (Hem.: Scutelleridae).
Scelionidae), which comprised about 70% of the parasitoids collected from Sunn pest eggs in Iran (Amir-Maafi, 2000; Amir-Maafi & Parker, 2002, 2003; Amir-Maafi, 2023; Yasemi et al., 2016).

Research towards understanding the natural occurrence of Sunn pest egg parasitoids for biocontrol of E. integriceps has been recently given attention in IRAN (Amir-Maafi, 2000). Success in conserving these natural enemies, especially T. grandis requires knowledge of the biology and ecology of these important parasitoids. A predictive model of seasonal phenology would significantly improve the T. grandis conservation. Predicting the seasonal occurrence of T. grandis requires quantifying the relationship between its immature stage development and temperature. However, little information is available on the thermal performance of this species (Amir-Maafi, 2000). In previous studies by Taghadosi (1991), Amir-Maafi (2000), Amir-Maafi & Parker (2011), and Nozad Bonab et al. (2014), development time, longevity, and fecundity were investigated under a limited range of temperatures. Although these previous studies provide valuable information on T. grandis temperature development, more data are needed to develop stage emergence models.

Consequently, the objectives of this study were to quantify the development of T. grandis concerning temperature and to establish stage emergence models for the conservation of T. grandis. Stage-emergence models also will be important components in a T. grandis population dynamics model.

Materials and methods

Insect culture

Egg masses of Sunn pest, E. integriceps were collected in wheat and barley fields in Varamin, Iran, during the growing season (from April to May 2021). Each egg mass was placed in a glass tube (1 cm diameter and 10 cm length) in a growth chamber (25±1 °C, 65±5 %RH, 16L:8D h). A piece of cotton with drops of water was put in the tube to keep the egg mass from desiccating. After four days, the parasitized eggs completely became black. The healthy egg masses were removed, and the parasitized masses were kept in the tubes. 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 16L:8D h in 20×14×7 cm polystyrene boxes for about eight 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 16L:8D h photoperiod for one generation. Afterward, newly-emerged adult parasitoids (F2) were used for the experiment. One hundred pairs of newly-emerged wasps, (<4 h-old) were placed individually into a glass tube (1 cm diameter and 10 cm length) containing one E. integriceps egg mass (14 eggs per mass) and held in a growth chamber (25±1 °C, 65±5 %RH, 16L:8D h). After four h, the wasps were removed and the parasitized eggs were placed in growth chambers held at one of the following temperatures: 12.5, 15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5, 35, 37.5 and 40 °C (±0.5), 65 ± 5% RH., and a photoperiod of 16L:8D h photoperiod for one generation. Afterward, newly-emerged adult parasitoids (F2) were used for the experiment. One hundred pairs of newly-emerged wasps, (<4 h-old) were placed individually into a glass tube (1 cm diameter and 10 cm length) containing one E. integriceps egg mass (14 eggs per mass) and held in a growth chamber (25±1 °C, 65±5 %RH, 16L:8D h). After four h, the wasps were removed and the parasitized eggs were placed in growth chambers held at one of the following temperatures: 12.5, 15, 17.5, 20, 22.5, 25, 27.5, 30, 32.5, 35, 37.5 and 40 °C (±0.5), 65 ± 5% RH., and a photoperiod of 16L:8D h photoperiod. The glass tubes were examined once every day, and the sex and number of adults that emerged were recorded at the time of emergence.

Development rate model

Linear model

Mean development rates were expressed as the reciprocal of development time (days) of the immature stage (egg to adult) of females, and males respectively. The standard regression method was fitted to the development rate. The lower temperature threshold and the thermal constant were calculated by solving the intercept/slope and 1/slope of the fitted equation for the immature stage.

Nonlinear development model

The development rates of the immature stage (egg to adult) of female and male, respectively were fitted to the modified Sharpe and DeMichele model (Schoolfield et al., 1981), because it is based on accepted biophysical laws and has parameters that can be interpreted biologically (Wagner et al., 1984a). This model is:

\[ r(T) = \frac{\rho25 \times (T/298.15) \times e^{[\frac{HA}{R} \times (1/298.15 - 1/T)]}}{1 + e^{[\frac{HL}{R} \times (1/TL - 1/T)] + e^{[\frac{HH}{R} \times (1/TH - 1/T)]}} } \]  

(1)

where \( r(T) \) is the developmental rate at temperature \( T \) (°K), \( R \) represents the universal gas constant (1.987 cal/degree/mol), \( \rho25 \) denotes the developmental rate at 25°C (298.15 °K) assuming no enzyme inactivation,
and $HA, TL, HL, TH$, and $HH$ represent the parameters of the kinetics of the rate-controlling enzymes. Parameters were estimated using the SAS program based on Wagner et al. (1984a).

**Distribution model of development time**

Variations in development time (egg to adult) of female and male, respectively for $T. grandis$ were fitted by a two-parameter Weibull function (Weibull, 1951; Wagner et al., 1984b; Cockeld et al., 1994):

$$ F(Px) = 1 - \exp \left( \frac{Px}{a} \right)^b $$

(2)

where $F(Px)$ is the cumulative proportion of stage emergence at physiological age $Px$, $a$ and $b$ are parameters.

Before fitting data to the Weibull function, cumulative frequency distributions for the development times of females, and males were constructed by adding the frequencies in successive ages of females, and males in days. Cumulative probability distributions were calculated by dividing the frequency of each age by the total frequency. Then, the age scale in days of females, and males was transformed to physiological age ($Px$) by the rate summation method (Curry & Feldman, 1987):

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

(3)

where $r(T)$ is the development rate at temperature $T$ (°K) of $i$th time step (e.g., day).

**Stage emergence simulation**

The stage emergence model, which predicts cohort emergence consist of the nonlinear development model and the distribution model of development time for each stage (Curry et al., 1978a, b). The development rate function determines the median (or mean) rate of development per day at a given temperature, while the distribution function determines the cumulative proportion of cohort development at a given accumulated development rate. The simulation was conducted using the computational method of Wagner et al. (1985). The cumulative emergence frequency of $T. grandis$ adults (males and females) was simulated using a two-parameter Weibull function (Eq. 2) based on physiological age ($Px$). Daily emergence probability was calculated by subtracting the cumulative proportion of the cohort shifted at $i$ from that of the cohort shifted at physiological age at $i+\Delta i$.

**Data analysis and line fitting method**

The effect of different temperatures on the developmental period of $T. grandis$ was analyzed by one-way analysis of variance (GLM) using SAS software. Means within treatments (temperatures) were compared by Tukey’s test. Parameters for the linear (REG Procedure) and nonlinear (PROC NLIN) were estimated using the procedure in SAS ver. 9.4 (SAS Institute 2019).

**Results**

**Temperature-dependent development**

The duration of the developmental period of immature stages of $T. grandis$ at different constant temperatures on Sunn pest eggs is given in Table 1. $T. grandis$ males and females developed successfully from egg to adult emergence from hosts over a range from 12.5-37.5 °C, except at 40 °C in this study. Statistical analysis manifested a significant influence of temperature on the egg–adult developmental time. Male parasites developed faster than female parasites at all temperatures at which emergence occurred (Table 1). The survival rate was maintained above 50% at all temperatures.

**Table 1.** Developmental time (in days) (mean±SE) of immature stage of females, and males of *Trissolcus grandis* at twelve constant temperatures.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Initial No.</th>
<th>No.</th>
<th>Female (day)</th>
<th>Male (day)</th>
<th>Survival (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>12.5</td>
<td>1400</td>
<td>639</td>
<td>78.429±0.067a</td>
<td>201</td>
<td>77.274±0.129a</td>
</tr>
<tr>
<td>15</td>
<td>1400</td>
<td>683</td>
<td>48.173±0.123b</td>
<td>207</td>
<td>45.115±0.123b</td>
</tr>
<tr>
<td>17.5</td>
<td>1050</td>
<td>655</td>
<td>26.704±0.049c</td>
<td>174</td>
<td>21.276±0.133e</td>
</tr>
<tr>
<td>20</td>
<td>1400</td>
<td>549</td>
<td>20.109±0.101d</td>
<td>186</td>
<td>19.172±0.198d</td>
</tr>
<tr>
<td>22.5</td>
<td>700</td>
<td>507</td>
<td>15.351±0.052e</td>
<td>174</td>
<td>13.897±0.074e</td>
</tr>
</tbody>
</table>
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The overall differences between treatments (temperatures) applied to each stage were tested by means of one-way ANOVAs with the associated test statistics given below in each column. Means followed by the same letter are not significantly different within columns (Tukey test, *P* < 0.01).

### Linear model

The estimated regression models were statistically significant and the relationship between developmental rate and temperature was described by linear regression equation for both sexes of *T. grandis* and results are shown in Table 2. The estimated low-threshold temperature was 10.62 °C for males, and 10.61 °C for females (Fig. 1, Table 2). The thermal constants of female, and males (development from egg to adult) were 179.85 and 161.03 DD, respectively (Table 2).

### Nonlinear model

Four-parameter Sharpe & DeMichele model with high-temperature inhibition, described the developmental rates of females, and males well as indicated by the high *r*^2^ values for the nonlinear regression (Fig. 1, Table 3). The estimated parameter values for females, and males (Table 3) were within the boundaries given by Wagner et al. (1984a). Values of *HA* were positive, and values of *RHO25*, which is the theoretical rate at 25 °C assuming no enzyme inactivation was closed the actual values at 25 °C in all cases. Values of *TH*, which enzyme is half active and half high-temperature inactive, were almost the same in all cases (Table 3). Also, the regression model was statistically significant for males (*F*=261.12, *df*=4,7, *P* < 0.0001), and females (*F*=494.98, *df*=4,7, *P* < 0.0001). The curves for females, and males showed a similar pattern. The development rates increased with increasing temperature up to a maximum development rate, and decreased sharply thereafter (Fig. 1).

### Distribution model

The cumulative distribution of development times for *T. grandis* (males, and females) against the physiological age is given in Fig. 2, and they fitted the two-parameter Weibull function. The high coefficient of determination achieved (*r*^2^>0.95) indicated that the function represented a good fit for *T. grandis* (females, and males) (Wagner et al., 1984b). Also, the regression model was statistically significant for males (*F*=585.88, *df*=2, 64, *P* < 0.0001), and females (*F*=967.31, *df*=2, 63, *P* < 0.0001). Overall distribution curves of *T. grandis* (females and male) had a similar shape (Fig. 2). The estimated parameter values of the distribution function are shown in Table 4. The value of parameter *b* was lower in the males than that of the females, indicating that males development time was more variable.

### Table 2. Developmental threshold and thermal requirement of immature stage of female and male of *Trissolcus grandis*.

<table>
<thead>
<tr>
<th>Sex</th>
<th>Parameter of linear model (±SE)</th>
<th>Lower threshold Temperature, °C (T_{b})</th>
<th>Thermal Constant, DD (k)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>a</em></td>
<td>0.059±0.005</td>
<td>0.006±0.0002</td>
</tr>
<tr>
<td>Female</td>
<td><em>b</em></td>
<td>0.066±0.009</td>
<td>0.006±0.0004</td>
</tr>
</tbody>
</table>

*The the overall differences between treatments (temperatures) applied to each stage were tested by means of one-way ANOVAs with the associated test statistics given below in each column. Means followed by the same letter are not significantly different within columns (Tukey test, *P* < 0.01).*
Fig. 1. Development rate (d⁻¹) curve for immature stage of females, and males of *Trissolcus grandis* as a function of temperature. The Sharpe and DeMichele (1977) biophysical model modified by Schoolfield et al. (1981) model was used.

**Table 3.** Estimated values of parameters in development model of immature stage of females, and males of *Trissolcus grandis*.

<table>
<thead>
<tr>
<th>Immature stage of</th>
<th>Parameter</th>
<th>Estimated value</th>
<th>SEM</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>RHO25</td>
<td>0.093</td>
<td>0.013</td>
<td>0.997</td>
</tr>
<tr>
<td></td>
<td>HA</td>
<td>21635.7</td>
<td>3678.7</td>
<td></td>
</tr>
<tr>
<td></td>
<td>HH</td>
<td>47226.7</td>
<td>6683.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>TH</td>
<td>305.7</td>
<td>2.336</td>
<td></td>
</tr>
<tr>
<td>Male</td>
<td>RHO25</td>
<td>0.125</td>
<td>0.042</td>
<td>0.993</td>
</tr>
<tr>
<td></td>
<td>HA</td>
<td>24922.9</td>
<td>7334.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>HH</td>
<td>40036.9</td>
<td>5522.6</td>
<td></td>
</tr>
<tr>
<td></td>
<td>TH</td>
<td>303</td>
<td>4.9035</td>
<td></td>
</tr>
</tbody>
</table>

**Table 4.** Estimated values of parameters in distribution model of development time for immature stage of females, and males of *Trissolcus grandis*.

<table>
<thead>
<tr>
<th>Immature stage of</th>
<th>Estimated value of parameter (±SEM)</th>
<th>F-value (df)</th>
<th>P</th>
<th>r²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>a = 0.987±0.007</td>
<td>b = 10.156±1.136</td>
<td>967.31 (2, 63)</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Male</td>
<td>a = 0.984±0.016</td>
<td>b = 5.466±0.796</td>
<td>585.88 (2, 64)</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
Fig. 2. Cumulative proportion of females, and males of *Trissolcus grandis* that completed development as a function of physiological age. Two-parameter Weibull function was used.

**Simulation of emergence pattern**

The simulation of *T. grandis* individuals in a cohort shifting from egg to adult concerning cohort age and temperature is provided in Fig. 4 for both females and males individuals. These simulation models enable us to predict when the adult emergence upon immature stage completion would occur over the full range of constant temperatures (Fig. 4). At optimum temperatures the emergence density curve exhibited lower variance and the shortest time for the emergence. At very low and very high temperatures, the emergence time would be delayed with higher variation among cohorts.

**Discussion**

Temperature is one of the main environmental factors that directly influence the development and survival of insects (Campbell *et al.*, 1974; Logan *et al.*, 1976; Sharpe and DeMichele, 1977; Schoolfield *et al.*, 1981; Wagner *et al.*, 1984a; Lactic, *et al.*, 1995; Briere *et al.*, 1999; Ikemoto, 2005, 2008 and Shi *et al.*, 2011). An understanding of these effects can significantly aid the interpretation of species phenology (Walgama & Zalucki, 2006), population dynamics (Huffaker *et al.*, 1999), and geographic distribution (Davis *et al.*, 2006). Developmental rate models, driven by temperature, have been extensively used to quantify the potential influence of temperature on insect development (Rebaudo & Rabhi, 2018). These phenology models can be valuable tools to determine the timing of key life history events at various spatiotemporal scales (Ehrlén & Morris, 2015). They can also be used to evaluate the response to variable and changing climate in insects and their population dynamics (Li *et al.*, 2016).
Fig. 3. Simulation temperature-dependent pattern of emergence of *T. grandis*.

The influence of twelve constant temperatures (12.5-40 °C) on the development time of the immature stage of females and males of *T. grandis* was evaluated in the current study. Results showed that temperature significantly affected the preadult development time of both sexes, decreasing when temperature was increased from 12.5 °C to 32.5 °C. Previously too, a direct influence of temperature on developmental rate has been reported (within a limited range of constant temperatures) for *T. grandis* (Amir-Maafi, 2000; Iranipour et al., 2010; Nozad Bonab et al., 2014) and for various species of *Trissolcus* (Powell et al., 1981; Yeargan, 1983; Torres et al., 2002; Kivan & Kilic 2005 and 2006a, b; Kasraii, 2010).

The current study investigated the relationship between temperature and the development rate of *T. grandis* and constructed a linear model for a wide range of constant temperatures. The relationship between temperature and the development rate of insects is often described by a linear regression equation. Although insects live under fluctuating temperatures, studies carried out under constant temperatures produce results that can still be used to understand the population dynamics of various insects (Summers et al., 1984).

Knowledge of thermal requirements allows us to expect the number of generations, the best time release of *T. grandis*, and its conservation (Amir-Maafi, 2000). In the present work, lower temperature thresholds and thermal requirements of *T. grandis* were calculated according to the linear model. The results showed that the lower temperature thresholds and thermal requirements values for the immature stage (egg-adult) of males and females were 10.62, 10.61 and 161.03, 179.85 d, respectively. However, these values differ from those previously reported by Iranipour et al. (2010), who found the lower developmental threshold temperatures for immature stages (egg-adult) of two populations of *T. grandis* to be 14.4 and 14.5°C (Qaramalek population) and 12.5 and 12.1°C (Bonab population) for males and females, respectively. The threshold temperature is often determined empirically by extrapolating a straight line to the temperature axis (Krogh, 1914), which...
may cause different threshold temperatures according to temperature ranges included by researchers. Iranipour et al. (2010) did not examine temperatures < 20 °C or > 32 °C and estimated lower threshold temperatures without data points < 20 °C, whereas our estimates included observations at temperatures < 20 °C; therefore, our results are likely more accurate. The results of this study will provide a better framework for reliable forecasting of T. grandis phenology, as these thermal parameters include biological details at low temperatures.

Nonlinear models can be more realistic than linear ones for insect temperature-dependent modeling due to their ability to describe better the relationship between temperature and development rates over a wider range of temperatures. T. grandis development showed the typical characteristic of insect development, which is well described by the biophysical model of the four-parameter Sharpe & DeMichele model with high-temperature inhibition (Schoolfeld et al., 1981). The biophysical model assumes a single enzyme controlling development rate. The parameter values of TH indicate that developmental inhibition for males and females begins at almost the same high temperature. The parameter value of HH for the females was higher than the similar values of HH for males, reflecting a much higher sensitivity of females to higher temperatures than male of T. grandis (Fig. 1). Overall, the biophysical model of four-parameter Sharpe & DeMichele model with high-temperature inhibition (Schoolfeld et al., 1981) was an excellent fit to T. grandis development.

In previous studies, Amir-Maafi (2000) and Iranipour et al. (2010) used Stinner (Stinner et al., 1974) and logistic models respectively for temperature-dependent growth models for T. grandis. The Stinner model is an algorithm for temperature-dependent growth-rate simulation, which is a more advanced concept in the field of insect growth modeling. This model is an improvement over traditional logistic models, as it takes into account the effects of temperature on insect growth rates. The advantage of using the Stinner model for temperature-dependent growth models is that it provides a more accurate representation of the relationship between temperature and development rates, especially for insects (Shi & Ge, 2010). This is because it accounts for non-linear relationships between temperature and development rates, which can be more accurately captured by nonlinear models (Shi & Ge, 2010). In contrast, logistic models assume linearity between the dependent variable and the independent variables, which may not accurately capture non-linear relationships (Dee et al., 2020). However, Shi & Ge (2010) also highlight the limitations of the Stinner model, such as its sensitivity to the effects of temperatures at and above the critical thermal maximum, which can yield negative growth rates that are important for determining population dynamics. Despite these limitations, the Stinner model is still considered an advancement in the field of insect growth modeling, as it provides a more accurate representation of the relationship between temperature and development rates compared to traditional logistic models. The biophysical model of the four-parameter Sharpe & DeMichele model with high-temperature inhibition has been proposed in this study to describe the relationship between temperature and development rates for T. grandis. The advantages of using a biophysical model, for temperature-dependent development include providing a more accurate representation of the relationship between temperature and development rates compared to traditional linear models, improved prediction capabilities, adaptability to different insect species, ease of use, and insights into population dynamics (Kim et al., 2001; Rueda et al., 1990; White et al., 2009). Biophysical models are based on thermodynamic principles, which allow for better prediction of the temperature dependence of insect development. They can more accurately predict the effects of temperature on insect growth rates under various conditions, such as different temperature regimes and fluctuations (Hagstrum & Milliken, 1988, 1991).

The distribution of development times is a key component in developing realistic models for insect development. This function incorporates the stochastic aspects of insect development by normalizing the variation of the development times at various temperatures (Wagner et al., 1984b), and provides information on the proportion (or number) of insects completing development at different times (i.e., physiological age). This study described the quantitative information on the development variation of T. grandis by observing individual responses under laboratory conditions. The inherent variation of T. grandis development time herein is quantified by using the Weibull function. When the shape parameter (b) in the function is compared among sexes, the small value for males suggests that the variation in immature development time is greater than females. The high variation in the duration of immature development may play a substantial role in the seasonal occurrence of different sex simultaneously in the field. For many insect species, it has been observed that development time variation among individuals in a cohort is skewed toward longer times and that the underlying distributions against normalized times have identical shapes irrespective of temperatures (Curry et al., 1978a, b; Sharpe et al., 1981; Wagner et al., 1984b). Therefore, the Weibull function has described the distribution of development time variation (Regniere, 1984; Wagner et al., 1984b; Cockfield et al., 1994). The development time distribution function, particularly when applied to T. grandis, can be a valuable tool for
predicting the time of occurrence of this insect. The stochastic approach for modeling insect development is based on a single, temperature-independent distribution of normalized development times. This approach provides essential information for optimal release time and conservation for parasitoids such as *T. grandis*.

**Author Contributions**

The author confirms sole responsibility for the following: conceptualization, methodology, formal analysis, investigation, draft preparation, final review and edit, visualization, supervision, project administration and funding acquisition.

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**Data Availability Statement**

All data supporting the findings of this study are available within the paper.

**Acknowledgments**

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**Ethics approval**

Insects were used in this study. All applicable international, national, and institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by the author.

**Conflict of Interests**

The author declares that there is no conflict of interest regarding the publication of this paper.

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