Predicting the population growth potential of Bactrocera zonata (Saunders) (Diptera: Tephritidae) using temperature development growth models and their validation in fluctuating temperature condition

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Abstract *Bactrocera zonata* (Saunders), a serious polyphagous pest of horticultural crops, was studied for temperature based growth potential at ecologically relevant constant temperatures (15, 20, 25, 30 and 35 °C; relative humidity of $60 \pm 10\%$ and a photoperiod of 12:12 h L:D) and simulated growth potential parameters were validated with fluctuating temperatures life cycle data under laboratory conditions on artificial diet. Rate summation and cohort updating approaches were used for simulating development and estimating life-table parameters of *B. zonata*. The results revealed that lower development thresholds as 11.9, 12.7, and 13.6 °C and optimum temperature for survival as 26.01 °C, 26.2 °C and 25.5 °C determined for eggs, larvae and pupae, respectively. Reduction in mean development time of all immature stages occurred with increase in temperature. The highest net reproductive rate (77.64 ± 2.59 females/female/generation), total fecundity (260.20 ± 6.37 individuals/female/generation), intrinsic rate of increase (0.10 ± 0.000 females/female/day) and finite rate of increase (1.10 ± 0.000 females/female/day) were obtained maximum at 30 °C. At lowest extreme temperature (15 °C) tested in present study, females were not able to lay eggs. The temperature between 25 and 28 °C was the most suitable range for *B. zonata* reproduction and development. This shows that temperature has significant role in determining the climatic suitability for *B. zonata* in reproduction.

Introduction

Bactrocera zonata (Saunders) commonly known as peach fruit fly, is a very severe pest of horticultural crops including peach (*Prunus persica* (L.) Batsch), guava (*Psidium guajava* L.), mango (*Mangifera indica* L.) in various countries (Hashem et al. 2001). Being multivoltine and highly polyphagous, *B. zonata* is reported to infest more than 50 fruit species of cultivated and wild plants (Duyck et al. 2004; OEPP/EPPO 2005). In India, it is considered as one of the most damaging fruit fly species causing 25 to 100% crop losses in peach, mango, guava, figs (*Ficus carica* L.) and apricot (*Prunus armeniaca* (L.) and widely distributed in the country from foothills

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of Himalaya to southern part (Gupta et al. 1990; Sanjeev et al. 2008; Choudhary et al. 2012). Combating the insect pest resurgence and outbreaks, pest forecasting models are very helpful in developing timely effective pest management strategies. Developmental time variability of insect pest life cycle generated under laboratory conditions can be simulated by temperature based growth models and these simulations can be useful for understanding the pest behavior under future climate change scenarios (Wagner et al. 1984). Heat unit accumulation above lower threshold temperature based linear degree day models were already developed for understanding growth stage development of *B. zonata* (Duyck et al. 2004; Ahmed et al. 2007; Fetoh et al. 2012). Optimum temperature requirement for insect development can be estimated through non-linear relationship between development of insect and tested temperature regime (Briere et al. 1999). Previous studies predicted the population growth of *B. zonata* on temperature-dependent models mainly concentrated on developmental thresholds, thermal constants and future risk assessments based on area suitability (Duyck et al. 2004; Ahmed et al. 2007; Fetoh et al. 2012; Ni et al. 2012). These simulation studies were not given the systematic emphasis on temperature based variation on developmental time, mortality and fecundity of *B. zonata.* Stochastic functions included in non-linear growth model can provide better simulation results of variability in development times with higher biological significance within a population (Logan et al. 1976; Sharpe et al. 1977; Sporleder et al. 2004). Using Geographic Information System (GIS) algorithms, the spatial simulation of the phenology model allows the climate change related prediction of insect population dynamics in various agro-ecological regions (Kroschel et al. 2013). Thus far, development of *B. zonata* specifically affected by daily and seasonal temperature extremes are not much understood. Extreme ranges in daily and seasonal temperature are very essential for the estimation of population growth potential in response to temperature and also help in understanding the climate change impacts on future population growth.

The main objective of present study was to generate basic information on ecology and temperature-dependent population growth phenology model for *B. zonata* that can be further used for risk assessments of this polyphagous species of pest.

Materials and methods

Fruit fly culture

The colony of *B. zonata* was established at ICAR-Research Centre for Eastern Region, Research Centre, Ranchi (Jharkhand) India. For colony set up, initially infested mango fruits were collected from ICAR-RCER, RC, Ranchi research farm during mango season of 2012 (23. 45° N, 85.31° E, elevation 620 m AMSL). Collected fruits were placed in insect rearing cages (30x30x30 cm size) along with sand at bottom for pupation. Newly emerged adult flies of *B. zonata* were placed in Perspex cages (Bio-agent acrylic cage of Rescholar equipment, India) (size: 30x30x30cm) for rearing and egg laying. Adults were provided semi-solid mixture of sugar (3 parts) and protein hydrolysate (1 part) as food and wet cotton as water source. Eggs were collected using plastic cups containing pieces of sponge saturated with host fruit juice (mango, guava and peach) with numerous pin pointed small holes (0.8 mm diameter). Collected eggs were placed with the artificial diet (500 g wheat bran, 200 g granulated sugar, 70 g brewer's yeast, 15 g agar, 2.0 g Methyl paraben, 1.8 g sodium benzoate and 1000 ml water) as suggested by Qureshi et al. (1974) with slight modifications. Three generations of *B. zonata* population was reared before starting the experiments. The laboratory colony of *B. zonata* was maintained at 25 ± 1 °C temperature, 60 ± 10% RH and 12:12 L: D photoperiod.

Development time and survival rate of eggs, larvae and pupae of *B. zonata* at constant temperature treatments

Development of *B. zonata* was studied at 15, 20, 25, 30 and 35 °C (± 1.0 °C) with 60 ± 5% RH and 12 h repeated light and dark photoperiod in thermostatically controlled environmental chambers (M/s. Saveer Biotech Ltd., India). The environmental chambers were illuminated with fluorescent light tubes. Fifty counted eggs were selected randomly with the help of fine brush, and carefully lined on pre-sterilized moistened black cloth for hatching and maintained in 4 replications. Fifty randomly selected newly emerged (nearly1h old) larvae of fruit flies were collected from culture and transferred carefully into plastic cups containing artificial diet with the help of camel hair brush. The number of egg hatched from fifty eggs in each replicate was observed twice a

day under a microscope for determining the percent egg hatching and incubation period. Newly formed pupae were observed daily in sand, later separated from the sand by gentle sifting. At 24-h intervals, observations for larval duration, pupal duration and adult emergence were recorded. Temperature-dependent development was also observed for insect mortality/survival. We replicated each experiment for 4 times.

Oviposition period, daily oviposition rate, fecundity and adult longevity

Newly emerged ten pairs of adult were placed in the Perspex cages along with adult diet described previously for observations of oviposition period, daily oviposition rate, fecundity and adult longevity. We monitored cages/plastic cups on a daily basis for recording data on oviposition period, daily egg laying and adult longevity.

Data analysis and phenology models parameterization

For generating the temperature dependent development and growth phenology model, Insect Life Cycle Modeling (ILCYM, version 4.0) software, developed by International Potato Centre, Lima, Peru was used (Sporleder et al. 2017). The ILCYM 4.0 works only with interval type data.

Development time and rate

Development rate distributions of different stages of *B. zonata* were estimated at various constant temperatures. Hypothesis used for development rate estimation was that the standard deviation of the development time is proportional to the median or mean of each distribution (Sharpe et al. 1977; Curry et al. 1978; Fand et al. 2014). The non-linearity in development rates of immature stages (egg, larvae and pupae) were fitted with Janish-1 at temperature extremes.

$$\text{Janish}-1 \; r(T) = \frac{2}{D_{min}\left(e^{k\left(T-T_{opt}\right)} + e^{-k\left(T-T_{opt}\right)}\right)}$$

(r(T) is the development rate at temperature T (°C), e is the natural exponential, T_{opt} is the temperature optimum and D_{min} and k are the model fitting parameters).

Lower development temperature thresholds and degree days for immature stages of *B. zonata* were estimated from slope and intercept of linear degree days

model while establishing the relationship between development rate and temperatures (Sporleder et al. 2004).

$$r(T) = a + bT$$

$$K = 1/b$$

(r(T) is the development rate (1/days) at temperature T (°C), a is the intercept and b is the slope; K is number of degree days thermal constant summed above theoretical lower development threshold (T_{min} ($= -a/b$) for the development period).

The adult senescence rates (adult life span) were plotted between inverse of survival time of female and male adults and temperatures by fitting simple exponential model.

Exponential simple $r(T) = b_1 \, \text{X} \, e^{b_2 \, \text{X} \, T}$

(r(T) is the development rate at temperature T (°C), e is the natural exponential, b_1 and b_2 are parameters to be estimated).

Complementary log-log (Cloglog) (egg and pupae) and Weibull (larvae, male and females) distribution curves were fitted and plotted against temperatures and normalized development of *B. zonata* for cumulative frequency of development times (Sporleder et al. 2017).

Cloglog distribution: $F(x) = 1 - exp\,(-\,exp\,(a_i + blnx))$.

Weibull distribution: $F(x) = 1 - exp^{-\left(\frac{x_i}{b}\right)^a})$

(Where, $F(x)$ is the probability to complete development at time x, lnx is the natural logarithm of the days observed, a is the intercept corresponding to temperature i, and b is the common slope of the regression model).

Wang model was best fitted for estimating mortality in immature life stages of *B. zonata* at different constant temperatures (Wang et al. 1982). Mortality rate refer here in each life stage for each temperature where number of individuals used and the number of individuals were not able to develop in to next stage.

$$m(T) = 1 - \frac{1}{e^{\left(\left(1+e^{\left(\frac{T-T_{opt}}{B}\right)}\right) X \left(1+e^{\left(\frac{T_{opt}-T}{B}\right)}\right) X H\right)}}$$

(Where, $m(T)$ is the mortality function at temperature T (°C), B and H are the model fitted parameters and Topt is the temperature optimum at maximum cohort survival).

Reproduction parameterization

The temperature dependent function of fecundity was considered for oviposition modelling. A Wang model was fitted to observe the various constant temperature effects on total egg produced by single female of *B. zonata* during her entire life span (Wang et al. 1982).

$$E(T) = 1 - \frac{1}{e^{\left(\left(1+e^{\left(-\frac{T-T_{opt}}{B}\right)}\right) X \left(1+e^{\left(-\frac{T_{opt}-T}{B}\right)}\right) X H\right)}}$$

(Where, $E(T)$ is the total eggs laid by the a female adult in total life span at given temperature T (°C); B and H are the model fitted parameters and T_{opt} is the temperature optimum at maximum egg laid by cohort)

Akaike's Information Criterion (AIC) and multiple coefficient of determination (R^2) were considered for the best fit models/functions selection.

Life table parameters simulation

Life table parameters (finite rate of increase (λ), gross reproductive rate (GRR), mean generation time (T), intrinsic rate of natural increase (r_m), net reproductive rate (R_o) and doubling time (D_t)) of *B. zonata* were simulated using simulation tool in ILCYM 4.0 (Curry et al. 1978). The stochastic constant temperature simulation for development, mortality and reproduction was performed with 100 individuals and 365 days over a range of 15–35 °C in 0.5° steps. The simulated life table parameters & respective temperatures were plotted against life table parameters and temperature constants. Significant differences were compared using Tukey test ($P > 0.5$) in SPSS 22.0.

Fluctuating temperature treatments and growth model validation

The life cycle of *B. zonata* was completed under the fluctuating temperatures condition. The daily temperature fluctuation in an incubator was between minimum 17 °C to maximum 32 °C at every 24 h. The minimum and maximum temperatures were maintained for 9 h periods and 3 h periods were provided for in between temperature fluctuation. Relative humidity (60 ± 10%) and photoperiods (12: 12 L: D) were maintained at constant temperature treatments. The range of temperature (17 °C to 32 °C) for fluctuation was selected by averaging year temperature records of Ranchi for two consecutive years i.e. 2011 and 2012. It covers the ranges from low to high temperature of weather data of Jharkhand state, India. The rearing procedures were same as adopted for constant temperatures except temperature fluctuation. The same two years (2011 and 2012) averaged temperature data were used for stochastic fluctuating temperature simulations of life table parameters in ILCYM. The fluctuating temperature dependent recorded life cycle data were used for validating the life phenology model generated through stochastic simulation at constant temperatures. Simulated values on development, mortality and reproduction were validated with experimental data observed on life cycle generated in fluctuating temperature treatment based on *p* value significance in the present study.

Results

Development time and rate

Each stage of *B. zonata* individuals were able to develop in to its estimation constants ranged from 15 °C to 35 °C temperature and the development time from egg to adult stage were largely affected by temperature (Table 1). The development time remarkably decreases with increase in temperature constants. Immature life stages i.e. egg (1.18 ± 0.32 median days), larva (4.66 ± 0.26 median days) and pupa (7.71 ± 0.61 median days) were developed fast at 30 °C temperature constant while took longer time (egg: 10.81 ± 2.32; larva: 31.99 ± 1.38; pupa: 51.77 ± 3.34 median days) for development when reared at 15 °C. Adult (female and male) longevity decreased remarkably with increasing temperature > 15 °C (Table 1). Weibull and complementary log-log distribution model parameters were fitted for explaining the cumulative development time and longevity frequencies of different stages of *B. zonata*, based on the lowest AIC values (Table 1). The highly significant ($P < 0.001$) common slopes were determined which seem to be adequately describe the overall variability in the development times within each life stage (Table 1). Non-linear equations based fit of curvilinear response of temperature and its extremities were used to describe the temperature dependent development of three immature life stages of *B. zonata*. The thermal reaction norms were well fitted with Janish-1 model as indicated by the highest value of coefficient of determination and smallest value of AIC for all immature life

Table 1 Development parameters of egg, larva and pupa and longevity and fecundity of adult female and male of *B. zonata*, at ecologically relevant constant temperatures studied under laboratory condition

Temperature (°C)	Egg		Larva		Pupa		Adult longevity (d)		Fecundity
	Med. dev. Time (d±Std. err.)	Survival (%)	Med. dev. Time (d±Std. err.)	Survival (%)	Med. dev. Time (d±Std. err.)	Survival (%)	Female med. Dev. time (d±Std. err.)	Male med. Dev. time (d±Std. err.)	Mean no. of eggs/female (no.±S. dev.)
15	10.81±2.32	33.70±3.80	31.99±1.38	43.68±4.00	51.77±3.34	41.70±4.00	135.04±11.62	105.71±811.01	NL
20	5.87±1.50	88.00±2.70	14.33±0.77	79.87±3.30	34.38±2.70	86.69±3.00	90.73±10.98	61.93±9.07	91.14±7.34
25	2.27±0.62	96.33±1.60	6.93±0.37	89.30±2.50	10.24±0.79	98.67±1.90	58.15±7.04	49.64±7.27	440.11±46.30
30	1.18±0.32	89.70±2.60	4.66±0.26	87.01±2.90	7.71±0.61	87.30±2.70	48.71±5.90	41.16±6.03	280.16±27.21
35	1.67±0.53	63.60±3.90	4.84±0.29	65.70±3.90	8.62±0.75	66.47±4.10	28.99±3.53	19.09±2.86	97.04±8.91
Model	Cloglog		Weibull		Cloglog		Weibull	Weibull	
Common slope	2.38±0.04		3.50±0.01		3.99±0.02		4.99±0.04	4.77±0.04	
AIC	2037.30		1625.37		2350.98		2178.35	2112.70	
$P(>|z|)$	<0.001		<0.001		<0.001		<0.001	<0.001	

stages of *B. zonata* (Egg, $P = 0.01$, F = 60.65, $df_{1,2}$ = 2,4; for Larva, $P < 0.001$, F = 1131.44, $df_{1,2}$ = 2,4 and for Pupa, $P = 0.04$, F = 22.86, $df_{1,2}$ = 2,4) (Table 2). Temperature dependent development non-linear equations parameters were calculated for egg, larva and pupal stages and presented in Table 2. Development rate increased invariably for all the immature stages until 31-32 °C later it reaches to peak and then, started declining (Fig. 1). Estimated lower development temperature thresholds from linear degree day's model were 11.9, 12.7 and 13.6 °C for egg, larva and pupae, respectively. Based on these lower temperature thresholds, the estimated degree-days for thermal constant (K), were 34.48, 111.12 and 198.87 degree-days for egg, larvae and pupae stages, respectively.

Immature mortality

The effect of temperature on immature stages of *B. zonata* mortality was well fitted with Wang models (Table 3 and Fig. 2). The percentage of eggs survival (hatching) ranged from 96.33 ± 1.60 (25 °C) to $33.70 \pm 3.80\%$ (15 °C) at various temperature cohorts. Maximum survival percentage of larvae ($89.30 \pm 2.50\%$) was recorded at the temperature 25 °C cohort and analogous trend was observed for the pupae (Table 1). At lower tested temperature (15 °C), relatively high mortality was observed for each immature stages of *B. zonata* with extended time interval of development (Fig. 2). The egg stage had shown the maximum differential response on mortality towards the changes in temperature regime as compared to other immature stages i.e. maximum mortality at 15 °C and maximum survival percentage at 25 °C (Table 1 and Fig. 2). The optimum temperature

with lowest mortality modelled by Wang models for eggs at 26.01 ± 0.18 °C (F = 136.64, df = 2, 4, $p = 0.007$), larvae at 26.24 ± 0.05 °C (F = 2775.00, df = 2, 4, $p < 0.001$) and pupae at 25.57 ± 0.20 °C (F = 81.36, df = 2, 4, $p = 0.01$) (Table 3).

Adult life span and fecundity

Stridently decreased of the longevity of both the adult sexes were observed from lower to higher tested temperatures (Table 1 and Fig. 3). Life span for adult male and female was statistically good fit in Exponential simple model with more than 0.90 values of regression equations for both sexes (Fig. 3). The significant effect of temperature was observed on the *B. zonata* reproduction. Predicted maximum total fecundity was around at 28 °C by fitted Wang model (F = 3305.50; $df_{1,2}$ = 2, 3; $p = 0.01$) (Table 4 and Fig. 4). Predicted maximum fecundity is matched with maximum fecundity i.e. 440 ± 30.1 egg/female observed at tested 25 °C temperature. At lowest tested temperature (15 °C), no egg laying was observed, indicating lower threshold are near to or surrounding within this temperature regime for *B. zonata* population.

Life table parameters at constant temperatures

The life table parameters at constant temperature were showed in Table 5. Data on life table parameters showed *B. zonata* attains a maximum net reproductive rate (R_0) (77.64 ± 2.59) at 25 °C temperature with maximum fecundity (260.20 ± 6.37) (Table 5). The mean generation time (T) notably differed from 38.32 ± 0.11 days at 35 °C temperature to $82.92 \pm$

Table 2 Parameters of non-linear models fitted to temperature-dependent development rate of all immature life stages of *B. zonata*

Life stage	Best fitted model	Model fitted parameters[a]	Parameters value (mean ± SE)	*F* cal	$df_{1,2}$	*P*	R^2 (adj R^2)
Egg	Janish-1	D_{min}	1.28 ± 0.15	60.65	2,4	0.01	0.98
		T_{opt}	31.30 ± 1.00				(0.97)
		K	0.18 ± 0.02				
Larva	Janish-1	D_{min}	4.32 ± 0.10	1131.44	2,4	<0.001	0.99
		T_{opt}	31.79 ± 0.27				(0.99)
		K	0.15 ± 0.00				
Pupa	Janish-1	D_{min}	7.28 ± 1.27	22.86	2,4	0.04	0.96
		T_{opt}	31.51 ± 1.76				(0.92)
		K	0.17 ± 0.02				

[a] fitted model Janish-1: T_{opt} is the temperature optimum and D_{min} and K are the model fitting parameters

Egg

a

Larva

b

Pupa

c
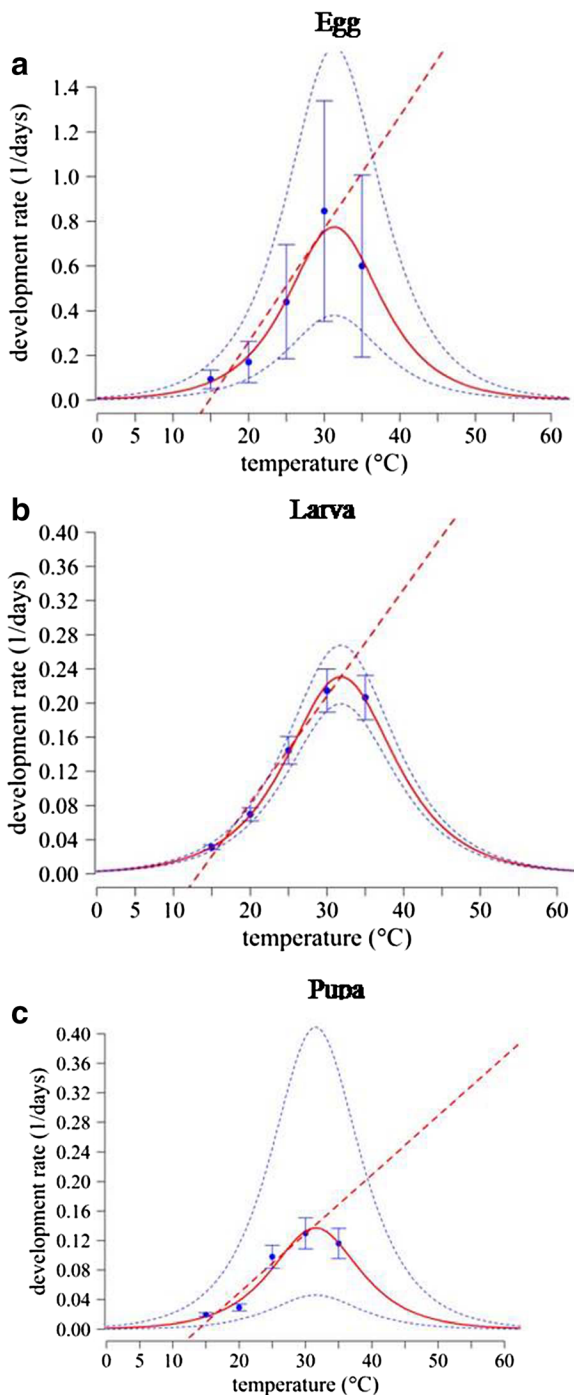
Fig. 1 Development rates (1/ day) of egg (**a**), larva (**b**) and pupa (**c**) of *B. zonata* at different constant temperatures with fitted Janish-1 model. The selected model output is indicated as bold solid red lines and dashed lines for the upper and lower 95% confidence bands. Bars point out standard deviation of the mean

Table 3 Parameters (mean ± SE) of the Wang fitted model to temperature dependent mortality rate for immature life stages of *B. zonata*

Parameters[a]	Egg	Larva	Pupa
T_{opt}	26.01 ± 0.18	26.24 ± 0.05	25.57 ± 0.20
B	2.37 ± 0.19	3.38 ± 0.04	2.60 ± 0.23
H	0.01 ± 0.003	0.02 ± 0.00	0.01 ± 0.01
F cal (df$_{1,2}$)	136.64 (2,4)	2775.00 (2,4)	81.36 (2,4)
p	0.007	<0.001	0.01
AIC	−16.97	−35.21	−15.20
R^2 (Adj R^2)	0.99 (0.98)	0.99 (0.99)	0.98 (0.97)

[a] Fitted Wang model: B and H are the model fitted parameters and T_{opt} is the temperature optimum at maximum cohort survival

1.61 days at 20 °C. At 30 °C, intrinsic rate of increase (r_m) and finite rate of increase (λ) were highest with values of 0.10 ± 0.000 and 1.10 ± 0.000, respectively. The minimum doubling time for completion of generation was 7.12 ± 0.05 days observed at 30 °C. The simulated parameters of life table of *B. zonata* were presented in Fig. 5. The ranges of temperature between 25 and 28 °C were observed most favorable for *B. zonata* survival, development and reproduction, with higher reproduction and quick completion of generations (Fig. 5).

Validation of model

The data on complete life cycle of *B. zonata* were generated using temperature fluctuations (17°- 32 °C) experiment with an average temperature of 24.5 °C. The phenology models fitted for immature life stage of *B. zonata* under constant temperatures predictions were analogous to those observed for immature life stages of *B. zonata* under fluctuating temperature experiments (Table 6). The trivial discrepancies were observed between D_t and GRR parameters of life table between observed and predicted experiments data. The life table parameters data predicted from simulated constant temperature experiment was significantly near with data observed from fluctuating temperature effect experiment.
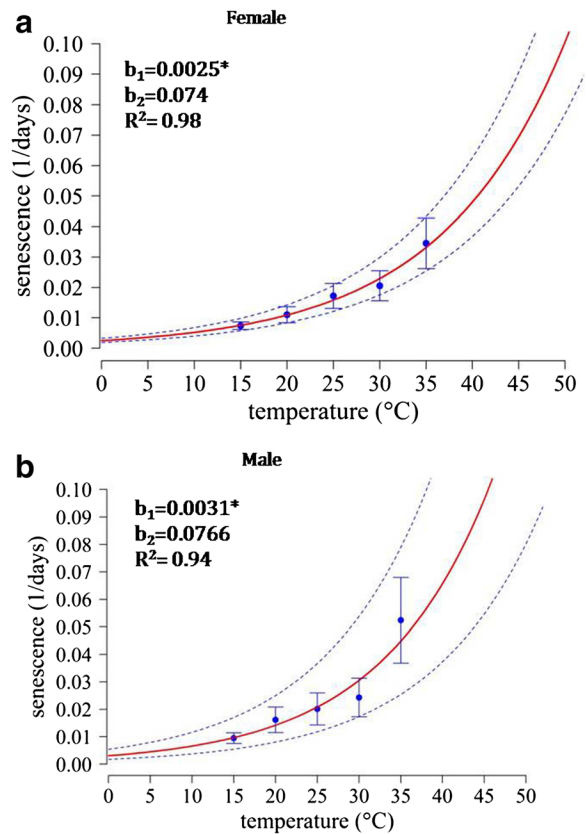
Discussion

Increase in temperature regimes changes the duration in completing the life cycle which helps insect species to
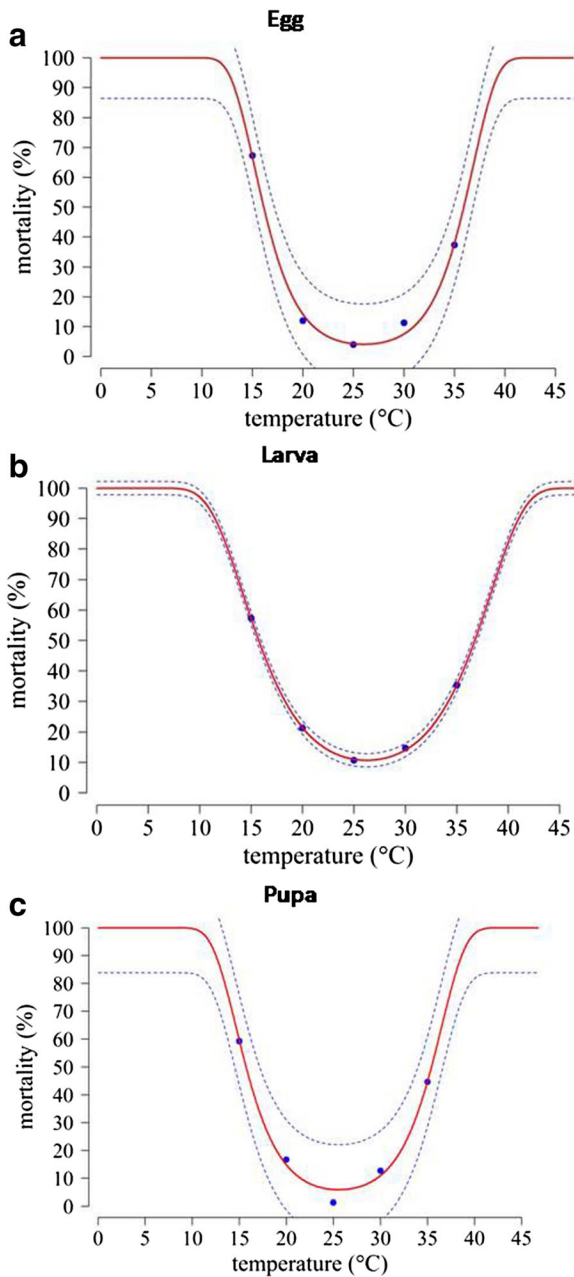
Fig. 2 Mortality rate of egg (**a**), larva (**b**) and pupa (**c**) of *B. zonata* at different temperatures fitted with the Wang model. The upper and lower 95% confidence intervals of the model are indicated

Fig. 3 Exponential simple model fitted senescence rate (1/days) for adult female (**a**) and males (**b**) of *B. zonata* at different temperatures. The upper and lower 95% confidence intervals of the model are indicated through dashed lines. Bars point out standard deviation of the mean

complete more generations within a short span of time. Understanding the biology and the population dynamics of insect pests would help in formulating and developing better and efficient pest control measures. Knowledge about life table parameters and occurrence of phenology events of insect are most important aspects for understanding the pest ecology. Temperatures

dependent growth development of insects can be assessed using the phenology model develop for life table parameters estimation. In the present study, the temperature-dependent life table parameters of a polyphagous pest, *B. zonata* were described using temperature dependent phenology modelling approach. It is already reported that temperature had significant influences on all the immature stages of *B. zonata* and well confirmed the linear relationship between temperature (15 °C and 30 °C) and time of development (Mohamed 2000; Duyck et al. 2004; Ahmed et al. 2007).

The present study revealed that the most favorable temperature for *B. zonata* development was between 25 °C and 28 °C but it can also maintain the development under constant temperatures ranged between 20 °C and 35 °C. Egg laying of *B. zonata* were not observed at 15 °C temperature constant. However, ovarian maturity at lowest temperatures extreme (15 °C) was also not reported by Duyck et al. (2004). Earlier studies by

Table 4 Parameters of the Wang model function fitted to fecundity per female of *B. zonata*

| Response variable	Wang polynomial function parameter values[a]						
	T_{opt}	B	H	F cal $(df_{1,2})$	P	AIC	R^2 (adj R^2)
Fecundity/female	28.85 ± 0.04	3.65 ± 0.03	-5861.67 ± 44.52	$3305.50 \ (2,3)$	0.01	23.95	0.99 (0.99)

[a] Fitted Wang model: B and H are the model fitted parameters and T_{opt} is the temperature optimum at maximum cohort survival

Duyck et al. (2004); Ahmed et al. (2007) and Fetoh et al. (2012) were not the studied the life table parameters of *B. zonata.* They mainly concentrated on effect of constant temperature on rate of development, immature mortality and in few cases on fecundity (only by Ahmed et al. 2007) and estimation of thermal constants. In the current study, the population growth parameters i.e. development rate, mortality at various stage and fecundity parameters were predicted by taking an account total life history under a given constant temperature regimes which are considered highly significant in understanding the pest population dynamics of variety of insect pests (Wagner et al. 1984; Sporleder et al. 2004; Srinivasa Rao et al. 2014; Fand et al. 2015).

The lower temperature thresholds, 11.9 °C for eggs, 12.7 °C for larva and 13.6 °C for pupa with respective 34.48, 111.12 and 198.87 degree-days thermal constant for *B. zonata* development from present study were slightly deviated or in closer concurrence with earlier studies (Mohamed 2000; Duyck et al. 2004; Ahmed et al. 2007; Fetoh et al. 2012). The trivial deviations that happen in lower temperature thresholds may be reasoned due to differences in strain used and by the type of food provided for rearing. In contrary to earlier studies, not

only lower temperature thresholds for the immature life stages of *B. zonata* were estimated but optimum temperatures for development (T_{opt}) were also estimated in present study. At different constant temperatures, the developmental duration of different stages of *B. zonata* observed were fairly well in range with earlier reports (Mohamed 2000; Duyck et al. 2004; Ahmed et al. 2007; Fetoh et al. 2012) except slight deviation in extreme low and high temperatures. The slight variation among different studies may be due to aggregation of larvae cohort (Vargas et al. 1997) at low temperature and nutritive value difference in rearing food (Fernandes-Da-Silva and Zucoloto 1993). Significant variation was observed among survivability of immature stages of *B. zonata* at different constant temperatures. At extreme low temperature (15 °C), rate of mortality of all the *B. zonata* immature life stages was highest and was considered as highly unfavorable for survivability. Low survivorship of different stages at low temperature and not a drastic mortality at higher temperature (35 °C) indicating a preferences for warm climatic conditions as earlier observed by Duyck et al. (2004). This high temperature requirement of *B. zonata* as compares to co-existing species (*B. dorsalis*) may have the advantage in its own establishment into new environment.

Temperature has significant affects on the longevity and fecundity of adults. The duration of life cycle of the *B. zonata* adults were approximately 5–6 times shorter at higher temperature (> 35 °C) when compared to lower extreme temperature (15 °C), results in to considerable decrease in the reproductive phase. In this study, adult females were found to live longer than males and similar significant differences in adult life span between sexes were reported by Ahmed et al. (2007) and Fetoh et al. (2012). A highly temperature-dependent response was observed in present study for rate of cumulative oviposition and overall fecundity of *B. zonata*. At 28 °C, maximum fecundity (445.73 eggs/ female) was observed with a curvilinear response and decreased stridently at above and below this temperature. These life table parameter observations indicating that temperature can be play a major role
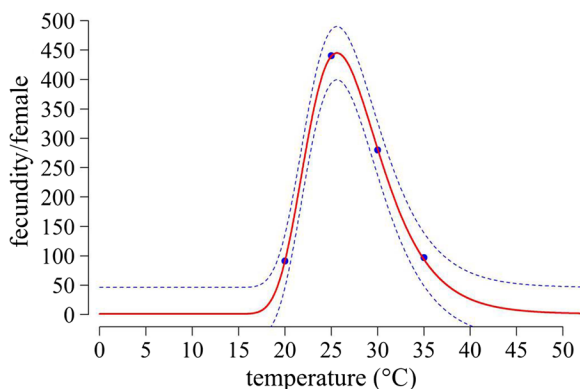
Fig. 4 Total egg production of *B. zonata* in relation to temperature variations. Fitted curve; Wang model, confidence intervals between upper and lower 95% of the model are indicated. The dots are observed data points
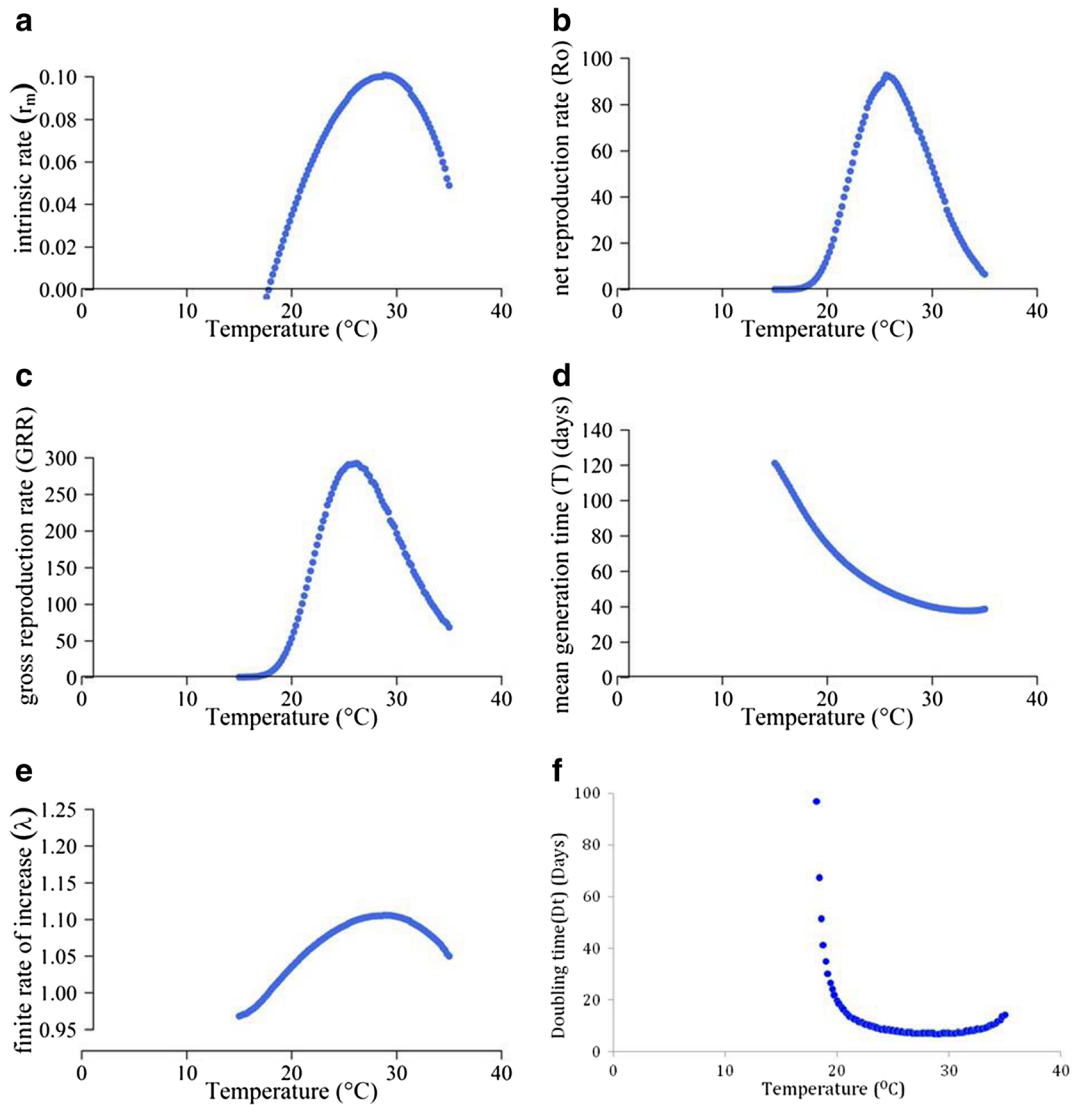
Table 5 Life table parameters of *B. zonata* at different examined constant temperatures

Temperature (°C)	r_m	R_o	λ	GRR	T	D_t
20	0.02 ± 0.003^a	6.17 ± 1.25^b	1.01 ± 0.003^a	26.04 ± 4.64^b	82.92 ± 1.61^a	41.34 ± 3.56^c
25	0.07 ± 0.003^b	56.47 ± 4.81^d	1.06 ± 0.003^b	185.23 ± 14.72^d	61.19 ± 1.38^b	11.20 ± 0.60^b
30	0.10 ± 0.000^c	77.64 ± 2.59^c	1.10 ± 0.000^c	260.20 ± 6.37^c	44.60 ± 0.64^c	7.12 ± 0.05^a
35	0.08 ± 0.003^b	24.85 ± 2.70^a	1.08 ± 0.003^b	122.59 ± 7.47^a	38.32 ± 0.11^d	9.07 ± 0.04^{ab}

Mean ± SE: standard errors are calculated from the simulated life table parameters

Means followed by same letter within columns are non-significant to each other ($p < 0.05$; Tukey's HSD test)

Net reproduction rate (R_o), Intrinsic rate of increase (r_m), finite rate of population increase (λ), gross reproduction rate (GRR), mean generation time (T), doubling time (D_t)

Fig. 5 Constant temperatures based simulated life table parameters of *B. zonata*. Intrinsic rate of natural increase (a), Net reproduction rate (b), Gross reproductive rate (c), Mean generation time (T), Finite rate of increase (e), and Doubling time (f)

Table 6 Validation between observed development and life table parameters in fluctuating temperature treatment and simulated parameters in diurnal temperature fluctuations

Parameters	Observed	Simulated values	p
Development time (days)			
Egg	1.62	1.52 ± 0.14	0.001
Larva	5.89	4.60 ± 0.28	0.003
Pupa	10.42	11.99 ± 1.36	0.038
Mortality (%)			
Egg	26.10	22.20 ± 1.12	0.374
Larva	21.60	24.20 ± 2.86	0.224
Pupa	34.50	37.50 ± 2.08	0.790
Life history parameters			
Net reproductive rate (R_o)	93.30	63.80 ± 17.05	0.087
Gross reproduction rate (GRR)	342.02	291.76 ± 25.62	0.016
Intrinsic rate of increase (r_m)	0.094	0.068 ± 0.016	0.058
Finite rate of increase (λ)	1.09	1.07 ± 0.017	0.057
Mean generation time (T) (days)	48.47	47.87 ± 2.12	0.180
Doubling time (Dt) (days)	7.41	10.16 ± 2.40	0.173

for mating and oviposition suitability of *B. zonata* adults. Temperature-dependent fecundity in present study was consistent with previous report stated that suitable temperature range for *B. zonata* reproduction is between 25 and 28 °C (Ahmed et al. 2007), and temperatures higher than 35 °C are having the detrimental effect (Duyck et al. 2004). For understanding insect population dynamics and developing the pests simulation models, in-depth knowledge of oviposition is very essential. The fecundity per female in our study are well in range but slightly lower in mean than those reported by Ahmed et al. (2007). Fecundity reported in this study are lower when compared with other tephritid species reported (*B. dorsalis* complex reared at 28 °C by Ekesi et al. 2006), but higher than for *B. cucurbitae* reared at 24 °C and at 29:18 °C those reported by Vargas et al. (2000). But several factors such as rearing conditions of larvae, adult nutrition, light intensity, age of stock culture, strain of population, adult senescence and even density of adults in rearing cages (Fernandes-Da-Silva and Zucoloto 1993; Vargas et al. 2000; Chang et al. 2004; Duyck et al. 2004; Ahmed et al. 2007; Fetoh et al. 2012; Shinwari et al. 2015), may mask the temperature effect on oviposition. Hence, fecundity of *B. zonata* reported in present study should be considered with some caution.

No work has been reported so far on effect of the different temperature constants on life table parameters of *B. zonata*, although similar work was reported with other tephritid species (Vargas et al. 2000; Papadopoulos et al. 2002; Ekesi et al. 2006). In this study, *B. zonata* had higher r_m value, indicating a daily increase of 7% and 10% at 25 °C and 30 °C, respectively as compared to *B. dorsalis* 6.5% reported at 24 °C (Vargas et al. 2000) it mean *B. zonata* has the more capacity to establish in the new environment. The r_m is described as a desirable trait in exploring for new environment (Ekesi et al. 2006). This gives an important advantage to *B. zonata* for interspecific competition over *B. dorsalis* and that is why it is surpassing population to next, as reported earlier in Bihar region of India (Agarwal et al. 1999). Previous literature also reported that slight irregularity in life table parameters with other species is due to deviations in selection of fitting sub models (Fand et al. 2014; Ekesi et al. 2006). At 25 °C to 30 °C, the population of *B. zonata* was estimated to double in 11.20 and 7.12 days which are comparable with the results reported by Vayssières et al. (2008) studied on *B. cucurbitae* whose population was estimated to double in 5.3 at 25 °C. The present results showed that values of r_o and r_m increases with raise in temperature from 20 to 30 °C. In contrast, mean generation time of cohorts declined with increasing temperature. The decline in generation time (T) at higher temperatures is due to shorten the immature stages development times and total average age of females. All the life table parameter equations are based on non-linear relationship and used for calculating upper and lower limits of parameters. Shorten generation time in response to increasing temperature of insect pests is the major reason and threat

to agricultural production systems, particularly in the tropical and sub-tropical region. Reduced mean generation time (T) in this study is in line to those of Ekesi et al. (2006) for *B. dorsalis* complex and Vargas et al. (2000) for *C. capitata* at 28 °C and 24:24 °C, respectively.

Conclusion

The temperature based phenology model in present study turn out into pertinent life table parameters for *B. zonata*. The phenology models of life table parameters of *B. zonata* using ILCYM software were estimated at constant and fluctuating temperature to reflect its growth potential in response to changes of temperature regimes. At the extreme low (15 °C) tested temperature, females of *B. zonata* were not able to lay eggs which exhibits the significance of temperature in mating and reproduction of *B. zonata* in response to suitable climate. Phenology model develop from present study can be linked with Geographic Information Systems (GIS) for mapping of pest population distribution, damage activity and population build up in response to climate change scenarios. Further, region specific risk assessment of *B. zonata* can also be modelled and could be proposed for adaptation planning in particular region.

Compliance with ethical standards

Disclosure statement   The authors declare no conflicts of interest.

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