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Temperature-based phenology model to predict the development, survival, and reproduction of the oriental fruit fly *Bactrocera dorsalis*

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ABSTRACT

The oriental fruit fly *Bactrocera dorsalis* (Diptera: Tephritidae) is a major pest of fruit and vegetable production systems on several continents. The pest has invaded many countries, causing considerable impact on fruit production systems and commercialization. In this study we determined the relationship between temperature and development, survival and reproductive parameters of *B. dorsalis* on an artificial diet under laboratory conditions under 7 constant temperatures (10, 15, 20, 25, 30, 33 and 35 °C) with 70 ± 10% relative humidity and a photoperiod of L12:D12. We validated the laboratory results with a full life table analysis under semi-natural conditions in a screenhouse. We used the Insect Life Cycle Modeling (ILCYM) software for all mathematical models and simulations applied to all life history parameters. *Bactrocera dorsalis* completed its development at temperatures ranging between 15 and 33 °C with the mean developmental time of egg, larva, and pupa ranging between 1.46 and 4.31 days, 7.14–25.67 days, and 7.18–31.50 respectively. The models predicted temperatures ranging between 20 and 30 °C as favorable for development and survival, and 20 to 25 °C for optimal fecundity of *B. dorsalis*. Life table parameters showed the highest gross reproductive rate (GRR), net reproductive rate (R_o), intrinsic rate of increase (r_m), and finite rate of increase (λ) between 25 and 31 °C while generation time (T) and doubling time (D_t) were low at this interval. The effects of future climate change on *B. dorsalis* life history parameters were further investigated and the outcome from this study will help in the management of *B. dorsalis* in different agroecologies in the context of ongoing climate change.

1. Introduction

The oriental fruit fly *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae) is among the most economically important tephritid species due to its widespread distribution and negative impact on production and trade of affected vegetable and tree fruits (Leblanc et al. 2013). *Bactrocera dorsalis* is highly polyphagous and has been reported on more than 300 species of commercial/edible plants and wild hosts with mango as the most preferred one (Allwood et al., 1999; Leblanc et al., 2013; Liquido et al., 2015). The fruit fly is a highly invasive species native to Asia but it is now found in numerous countries on several continents (Vargas and Leblanc, 2015). It was first detected in Africa on coastal Kenya in March 2003 (Lux et al., 2003) and was subsequently described as a new species, then named *Bactrocera invadens* Drew, Tsuruta and White (Drew et al., 2005). A decade later, based on morphological and molecular evidence, *B. invadens* was synonymized with *B. dorsalis* (Schutze et al., 2015). By 2018, the pest was reported from 35 countries in sub-Saharan Africa including Comoros and Mauritius islands (CABI, 2018; Mutamiswa et al., 2020), where it has become a major fruit pest of economic importance (Ekesi et al., 2006b; Mwatawala et al., 2006; Vayssières et al., 2015; Hanna et al., 2020). Today, *B. dorsalis* is found in 65 countries worldwide (CABI, 2020), including a first record of *B. dorsalis* in the Campania Region, Italy (Nugnes et al., 2018). Due to its high competivity, *B. dorsalis* has displaced the native *Ceratitis* species and has become the major fruit pest of economic importance in tropical Africa (Ekesi et al., 2009; Rwomushana

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et al., 2009).

The biology, ecology and management of *B. dorsalis* have been intensively studied in the field and the laboratory in many countries across the world. These studies focused on seasonal population dynamics (e.g., Mwatawala et al., 2006; Peng et al., 2006; Vayssières et al., 2015; Gnanvossou et al., 2017), eradication techniques and management (e.g., Ekesi et al., 2006; Vargas and Leblanc, 2015), and the effect of temperature on development, survival and reproduction at constant temperatures (Yang et al., 1994; Rwomushana et al. 2009; Luo et al., 2009; Salum et al., 2014; Danjuma et al., 2014) and alternating temperatures in controlled environments (Vargas et al., 2000). These studies showed that in general, the response of *B. dorsalis* to constant temperature under laboratory conditions varies from one population to another which could lead to differences in understanding and predicting distribution and abundance of *B. dorsalis* (Yang et al., 1994; Vargas et al., 1996; Rwomushana et al. 2009). Specifically, all the published studies on *B. dorsalis* response to temperature used linear degree-day models to predict the effect of temperature on the development of immature stages of *B. dorsalis*. The linear model has the advantage of simplicity and allows estimation of lower developmental threshold which is then used to estimate the degree-day required for development (Higley et al., 1986). However, the linear model often produces errors in the threshold estimates at the low temperature response spectra and are not appropriate to estimate upper threshold because of the typical non-linearity of development at high temperatures (Wagner et al., 1984; Brière et al. 1999). Non-linear models were developed to improve estimates of the lower and upper threshold development estimates.

In Africa, only two studies have focused on the effect of constant temperatures on immature development and demographic parameters of *B. dorsalis* (Rwomushana et al. 2009; Salum et al., 2014). Neither study emphasized simulation of developmental period, mortality and fecundity in response to temperature using non-linear functions which are more appropriate for estimating some demographic parameters of this pest. This study aims to predict the development, survival and reproduction of a Cameroonian population of *B. dorsalis* reared at 7 constant temperatures using non-linear models. These models will help to understand its population dynamics in environments with different temperature profiles to develop better management of the pest.

2. Methodology

2.1. Origin and establishment of B. dorsalis' colony

The initial cohort of *B. dorsalis* used in this study was obtained through incubation of 30 infested mango fruits (*Mangifera indica* L. var Camerounaise) collected in October 2011 in the orchard of the International Institute of Tropical Agriculture in Yaoundé, Cameroon (latitude 3°51′50.6766″N, longitude 11°27′ 45.3702″E, altitude 768 m) and maintained for three generations before the commencement of the thermal experiments. The mango fruits were incubated in 2-L containers lined at the bottom with pasteurized river sand as pupation medium. Collected pupae were kept in an insectarium maintained at 25 ± 1 °C, 70 ± 10 % RH and L12:D12 photoperiod. One hundred emerged adults were transferred to each of 2 cages with equal number of males and females. Adult cages (30 × 30 × 30 cm) were made of plexiglass and mesh (standard size) on the lateral sides for ventilation (Nanga Nanga et al., 2019). Adult flies were given a diet made of a mixture of enzymatic yeast hydrolysate (USB Corporation, Cleveland, OH), brown sugar (1:3 proportion) and distilled water (Ekesi et al., 2007). Eggs were collected from the initial laboratory population by exposing adults flies to a hollowed papaya dome (portion of papaya with pulp and seed removed) for 1 h. Eggs were removed from the inner side of the dome using a moist fine camel hairbrush (000). Newly hatched larvae were reared on a carrot-based diet (Ekesi et al., 2007) under the same room conditions until the third generation before using them in the experiments described below.

2.2. Experiments at constant temperatures

The development of immature stages and oviposition experiments were conducted in climate-controlled cabinets set (30-VL and 36-VL, Percival Scientific Inc, Perry, Iowa, USA) set at 7 constant temperatures (10, 15, 20, 25, 30, 33 and 35 ± 1 °C), L12:D12 photoperiod and 70–80 % RH. Temperature and relative humidity inside all climate cabinets were logged at 30-min interval by a HOBO Prov2 Temp/RH (Onset Computer Corp., Boume, MA, USA).

2.2.1. Development of immature stages

For the egg development experiment, a cohort (considered as a replicate) of 50 newly laid eggs (<1-h old) were placed on a 9.5-cm diameter moist black filter paper in a Petri dish and exposed inside the climate cabinet set at one of the 7 constant temperatures mentioned above. A total of 60 cohorts (i.e. replicates) were exposed at each temperature, for a total of 3000 eggs per rearing temperature. Egg development time was determined by monitoring egg hatch at 24-hr intervals until the last egg hatch.

For the larval development experiment, all first instar larvae obtained from each egg cohort were counted and transferred onto a surface of 50 g of a carrot-based diet in 50-ml plastic cups. Pupariating larvae could leave the rearing 50-ml cup *ad lib* into a large 150-ml plastic cup containing a layer of pasteurized sand in the bottom for pupation.

Pupae obtained daily from each larval cohort were kept in a lid-less 9.5-cm Petri dish and maintained inside the incubators for adult emergence. Pupae that did not hatch were dissected (after 2 weeks of their pupation) and classified as empty pupa or dead unhatched adult. Development time (in days) and number of individuals that reached the next life stage were recorded daily.

2.2.2. Adult longevity and reproduction

Adult flies used in this experiment were collected from the *B. dorsalis* laboratory colony that was maintained as described above. Ten *B. dorsalis* adult pairs (one-day-old male and female) of newly emerged adults (each group of 10 adult pairs representing a replicate) were held in a well-ventilated transparent Plexiglas cages (15 × 15 × 15 cm), and placed inside the climate cabinets set at one of the 6 temperatures (15, 20, 25, 30, 33 and 35 °C) with relative humidity and photoperiod as stated above. Ten replicates were used per temperature, for a total of 600 individuals (300 males and 300 females). Adults were provided with a 3:1 volumetric mixture of sugar and enzymatic yeast hydrolysate and distilled water. For each replicate, a small papaya dome, with at least 20 holes punctured by an entomological pin, was placed on top of a 5-cm Petri dish and replaced daily to follow female oviposition until the death of the last fly.

2.3. Development, survival and reproduction under semi-natural conditions

In order to validate the developed model under various temperatures, life table parameters of *B. dorsalis* were estimated under semi-natural conditions. To that end, a complete life table approach was conducted in a shaded screenhouse with ambient temperatures, relative humidity and photoperiod at the IITA-Cameroon experiment station in Yaoundé, Cameroon (see geographic coordinates above). The experiment was initiated with 300 newly laid eggs from the same *B. dorsalis* colony used for the lab experiments. The same procedure – as in the laboratory experiment - was repeated for immature development but following a complete life table approach in which a single egg was followed individually until the emergence of the adult which were randomly coupled (59 couples obtained) and kept in a well-ventilated 15 × 15 × 15 cm Plexiglas cage. The number of eggs laid by each female and the life span of both males and females were monitored daily. Temperature and relative humidity of the shaded house were logged at 30-min time interval using a HOBO Prov2 Temp/RH (Onset Computer

Corp., Boume, MA, USA) throughout the experiment, while the photoperiod was approximately L12:D12.

2.4. Model parameterization and data analysis

2.4.1. Modeling software

Life table data collected for this study were computed using the Insect Life Cycle Modeling (ILCYM, version 3.0), a software developed by the International Potato Center (Kroschel et al., 2013; Tonnang et al., 2013). ILCYM is made of three components: "model builder", "validation and simulation" and "analysis of mapping population". The phenology model of our study was developed by the "model builder" which contains several nonlinear functions to define the effect of temperature on insect's development. The best-fit models were selected based on the coefficient of determination (R^2) and the Akaike's Information Criterion (AIC) (Tonnang et al., 2013). Life table parameters were estimated with the "validation and simulation" module, which uses the phenology from "model builder" for deterministic and stochastic simulation of *B. dorsalis* population abundance under constant and fluctuating temperature.

2.4.2. Development time

Development times of *B. dorsalis* immature stages at each temperature were log-transformed and fitted to ILCYM's 3 cumulative density functions - the probit, the logit and the Complementary log-log (CLL) functions. The cumulative frequencies of developmental times of each life stage and temperatures were plotted against normalized developmental times. For our analysis, the probit function was used for egg, larva and pupa while the CLL function fitted well the longevity of male and female; their mathematical expressions are given by equations (1) and (2).

$$\text{Probit distribution } F(x) = \Phi(a_i + b \ln x) \tag{1}$$

$$\text{CLL distribution: } F(x) = 1 - e^{\left(-e^{(a_i + b \ln x)}\right)} \tag{2}$$

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. The best fit model was selected according to the lowest Akaike's Information Criterion (Akaike, 1973).

2.4.3. Development rate

The development rate of immature stages of *B. dorsalis* was expressed as the inverse of development times (in days) at each temperature. A linear and non-linear model was used for each immature stage. In the linear regression models, development rates of each immature stage were regressed against temperature in the R software version 3.5.1 (R Core Team, 2018). The model was expressed as:

$$r(T) = aT + b \tag{3}$$

where r(T) is the development rate at temperature T (°C), a is the slope, and b is the y-intercept. For each stage, lower developmental threshold was calculated as –b/a while the thermal constant in degree-day (DD) required to complete development was calculated as 1/a.

A non-linear regression was also applied to fit the development rate of all immature stages reared at the 7 constant temperatures regimes using the non-linear functions in ILCYM. For each immature stage, we applied these models and the choice of the best fitted function was based on Akaike's Information Criterion (AIC) (Akaike, 1973), the built-in statistics (R^2, adjusted R^2, and MSE) and also its biological sense. The smaller is the AIC value, the better the model reproduces the data trend. A Least Square Design (LSD) test was applied at $P = 0.05$ significance level for probability thresholds and hypothesis testing in all analysis in ILCYM.

The description of the development rate of eggs and pupa of *B. dorsalis* was performed using the following Briere 4 model (Briere et al., 1999) following the equation below:

$$R(T) = a(T - T_o)\,(T_{max} - T)^{1/n} \tag{4}$$

where, R(T) is the development rate at temperature T (°C), aa is an empirical constant, T_o is the lower temperature, T_{max} is the maximum temperature and *n* is a fitted parameter.

For the larva, the non-linearity of development at high temperature was estimated using the Briere 3 model (Briere et al., 1999) expressed as follow:

$$R(T) = a(T - T_o)\sqrt{(T_{max} - T)} \tag{5}$$

where, R(T) is the development rate at temperature T (°C), aa is an empirical constant, T_o is the lower temperature and T_{max} is the maximum temperature.

2.4.4. Survival rate of immature stages

Survival rate (percentage) of each immature stage and combined survival from egg to adults at each temperature was calculated by dividing the number of individuals that survived to the next stage by the initial number of individuals. Egg and larva survival rates at all temperatures were described well by the Polynomial 2 function expressed as:

$$S(T) = 1 - \left(e^{(b_1 + b_2 * T + b_3 * T^2)}\right) \tag{6}$$

where S(T) is the survival rate at temperature T (°C) and b_1, b_2, and b_3 are fitted parameters.

Pupa survival rates at all temperatures were well described by the Polynomial 4 function expressed as:

$$S(T) = 1 - \left(e^{(b_1 + b_2 * T + b_3 * \sqrt{T})}\right) \tag{7}$$

where, S(T) is the survival rate at temperature T (°C), b_1, b_2, and b_3 are polynomial function parameters.

2.4.5. Adult senescence

Senescence is used in ILCYM to denote adult survival and is estimated as the inverse of the mean survival time of both sexes at each temperature. The modified Stinner model (Stinner et al., 1974; Régnière et al., 2012) was used to estimate the effect of temperature on male and female senescence and was mathematically expressed as:

$$R(T) = \frac{C_1}{1 + e^{(k_1 + k_2 * T)}} + \frac{C_2}{1 + e^{(k_1 + k_2\ (2 * T_o - T))}} \tag{8}$$

where, R(T) is the senescence rate at temperature T (C), T_o is the optimum temperature (°C), C_1 and C_2 are the maximum and minimum temperatures (°C) when T - T_o and T > T_o, respectively, and $k_1$and k_2 are constants representing the slope and the intercept, respectively.

2.4.6. Adult female fecundity

The total number of eggs laid by each female was obtained by summing the daily number of eggs laid by each female throughout its lifespan. Daily mean fecundity was calculated as the total number of eggs laid per day divided by the number of females alive on that day; it was calculated until the death of the last female in each replicate. The relationship between temperature and mean total fecundity was described by the modified Wang model to determine the effect of temperature on total number of eggs laid per female. The mathematical expression of the model is as follow:

$$F(T) = 1 - \frac{H}{e^{\left(1+e^{\left(\frac{x-T_{opt}}{B}\right)}\right)\left(1+e^{-\frac{T_{opt}-x}{B}}\right)}} \quad (9)$$

where F(T) is the fecundity at temperature T($^{\circ}C$), T_{opt} is the optimum temperature (°C), H, B and x are fitted parameters.

The age specific fecundity rate was determined at each temperature tested. The gamma equation was used to plot the cumulative oviposition rate against normalized female age. The equation is expressed as follow:

$$F(T) = \int_0^T \left(\frac{1}{b^a \Gamma(a)} T^{a-1} e^{-\left(\frac{t}{b}\right)}\right) \quad (10)$$

where F(T) was the mean number of total eggs produced by a female at temperature T (°C), Γ is the maximum reproductive capacity, T is the temperature (°C) at which the maximum reproduction occurred, a and b are a fitted parameter.

2.4.7. Demographic parameters

Life table parameters were estimated using the 'stochastic simulation' tool in ILCYM. The procedure input the phenology model developed at eleven constant temperatures (15, 17, 19, 21, 23, 25, 27, 29, 31, 33 and 35 °C), starting with 100 individuals at the egg stage while assuming a 0.5 female progeny ratio. The following demographic parameters were estimated: 1) the gross reproductive rate (GRR) which is the average number of daughters produced by one female throughout its life span; 2) the intrinsic rate of natural increase (r_m) representing the percentage of growth of the population from one generation to another; 3) the net reproductive rate (R_o) that represents the number of individuals a single female can produce during its lifespan but takes into account the mortality rate of immature stages; 4) the mean generation time (T) is defined as the length of time requires by a population to increase to R_o-fold of its population size at the stable age; 5) the doubling time (D_t), is the time needed (in days) by one population to double; and 6) the finite rate of increase (λ) is the number of female offprint's produced by one female every day (Tonnang et al., 2013). The simulations were replicated 10 times for each temperature, representing 1000 individuals at egg stage.

2.4.8. Model validation

The phenology model was validated by estimating life table parameters at fluctuating temperatures. Daily data on minimum and maximum temperatures recorded under natural conditions at Yaoundé (11°5′ N, 3°86' E and 768 m) during the year 2013, were used for the validation of simulated and observed life table parameters of *B. dorsalis*. Only the results for Yaoundé are discussed here. Yaoundé was chosen because the annual minimum and maximum temperature of the year 2013 ranges between 14.7 and 35.3 °C which is close to the range of temperatures favorable for the development of *B. dorsalis*.

2.5. Statistical analysis

The effect of temperature on survival rate (percentage) of each immature stage was calculated by dividing the number of individuals survived to the next stage by the initial number of individuals at each temperature. Normality and homogeneity of variances were verified with Shapiro–Wilk and Bartlett tests. One-way ANOVA test was used - as data was normally distributed - to examine the effect of temperature on survival, development time of each life stage, and demographic parameters. The mean pre-oviposition period was estimated for each replicate as the number of days spent by females before the first oviposition event occurred. The Generalized Linear Model (GLM) with Gaussian distribution was used to examine the effect of temperature on pupation success, fecundity, longevity and pre-oviposition period using the "*glm*" function in R version 3.5.1 (R Core Team, 2018). After the ANOVA and the GLM procedures, means were separated by the Tukey HSD test ($P < 0.05$). The sex ratio was examined using the χ^2 test. All analyses were performed in R version 3.5.1 (R Core Team, 2018).

2.5.1. Results

2.5.1.1. Survival and development time of immature stages. Immature stages (eggs, larvae and pupae) of *B. dorsalis* completed their development at temperatures ranging between 15 and 33 °C. Out of 3000 eggs exposed, no larvae were obtained at 10 °C, and only 17 larvae were obtained at 35 °C, but none developed into pupa. Table 1 summarizes the effect of constant temperatures on survival of immature stages. Survival of *B. dorsalis* was significantly affected by temperature at all immature stages. At 15 °C, the survival rates of larvae and that of all immature stages combined were low (13.1 % and 5.37 % respectively) while at 33 °C, 77.1 % of larvae survived but only 1.27 % of the initial egg batch survived to adult stage. At intermediate temperatures (20, 25 and 30 °C), survival rates of immature stages were above 50 % while percentages of individuals that completed development were 33.90, 49.73 and 29.5 % at 20, 25 and 30 °C respectively. Temperature significantly affected the mean number of unhatched pupae expressed by empty pupae and dead flies (Table 1). Overall, the number of dead flies and empty pupae were significantly higher at 30 and 33 °C compared with low and intermediate temperatures (15, 20 and 25 °C) (Fig. 1).

The developmental time of immature stages of *B. dorsalis* was influenced by temperature and within the tested temperature range (15–35 °C), development time significantly decreased with increasing temperature up to 33 °C at which the development of eggs was significantly prolonged compared with 30 °C (Table 2). The variability of development times and adult survival was described by a cumulative probit distribution for egg ($R^2 = 0.99$; AIC = 266.6) and pupae ($R^2 = 0.99$; AIC = 1223.4), the logit distribution for larva ($R^2 = 0.98$; AIC = 1429.94), and the complementary log-log distribution for the longevity of males ($R^2 = 0.98$; AIC = 2350.2) and females ($R^2 = 0.97$; AIC = 7701) (Table S1).

2.5.1.2. Development rate of immature stages. The linear model described the linear portion of the development rate for eggs ($F = 875.5$; $df = 5$; $P < 0.001$, $R^2 = 0.79$), larvae ($F = 1506.0$; $df = 4$; $P < 0.001$, $R^2 = 0.89$), and pupae ($F = 886.2$; $df = 4$; $P < 0.001$, $R^2 = 0.96$) (Table 3). From the slope and the intercepts of the linear regressions, the lower development threshold temperatures estimated from each life stages (LTT = - intercept/slope) were 7.53, 6.25 and 7.00 °C for egg, larva, pupa respectively. The thermal constant obtained from these thresholds expressed in degree-day (DD = 1/slope) were, 31.3, 250.0, and 333.3 DD respectively for egg, larva, pupa (Table 3).

Out of the 59 models used to quantify the non-linear relationship between the development rate and extreme temperatures, the Briere 4 model was the best fit for eggs ($R^2 = 0.97$; $P = 0.035$; AIC = −17.90), and pupa ($R^2 = 0.95$; $P = 0.001$; AIC = −18.00) while the Briere 3 model fitted well for larva ($R^2 = 0.98$; $P = 0.015$; AIC = −30.81) (Fig. 2a, b and c; Table S2).

2.5.1.3. Mortality rate of immature stages. Temperature significantly affected the mortality rate of immature stages of *B. dorsalis*. The mortality rate varied between 27.4 % (15 °C) to 99% (35 °C) for egg (Fig. 3a), 22.3 % (33 °C) and 86.9 % (15 °C) for larva (Figs. 3b) and 44.4 % (15 °C) to 98.1 % (33 °C) for pupa (Fig. 3c). Parameters of the models applied for the mortality of immature stages are presented in Table S3. Our results show that the temperature-dependent mortality for the immature life stages was well described by the Polynomial 2 model with ($R^2 = 0.91$; $P = 0.007$; AIC = −3.50) for egg and Polynomial 4 model for

Table 1
The effect of temperature on survival rate of immature stages of *Bactrocera dorsalis* (mean (%) ± standard error).

Temperature (°C)	Egg		Larva		Pupa		Egg to adult	
	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE
10	(3000)	0.00 ± 0.00a		–		–		–
15	(3000)	72.60 ± 1.29b	(2177)	13.10 ± 1.62a	(286)	42.90 ± 4.95a	(159)	5.37 ± 0.90a
20	(3000)	80.23 ± 1.11bc	(2429)	54.58 ± 2.67b	(1320)	80.50 ± 2.74b	(1055)	33.90 ± 2.18b
25	(3000)	87.93 ± 0.67c	(2638)	65.51 ± 2.69c	(1733)	87.00 ± 1.61b	(1493)	49.73 ± 2.20c
30	(3000)	83.90 ± 0.67bc	(2516)	63.86 ± 2.34cd	(1599)	56.21 ± 2.65a	(885)	29.45 ± 1.67b
33	(3000)	87.73 ± 1.07bc	(2631)	77.08 ± 1.88e	(2045)	1.81 ± 0.55c	(38)	1.27 ± 0.43a
35	(3000)	0.47 ± 0.28a	(17)	0	–	–		–
F value		70.97		282.90		41.06		25.81
df value		6, 358		5, 298		5, 298		5, 298
p value		<0.001		<0.001		<0.001		<0.001

Values followed by a different letter in the same column are significantly different using the Tukey HSD test. ANOVA *F*, *df*, and *p* values are presented at the end of the table for each life.

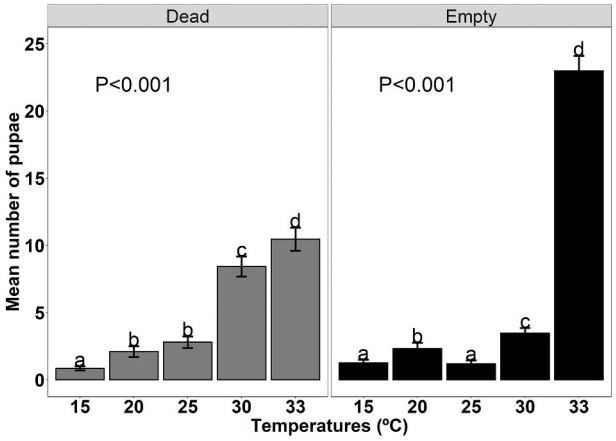


Fig. 1. Empty pupae and dead adult flies in dissected pupae from which no adult emergence was observed of non-eclosed pupae (no development occurred at 35 °C).

larva ($R^2 = 0.90$; P = 0.030; AIC = −3.83), and pupa ($R^2 = 0.99$; P = 0.007; AIC = −14.33).

2.5.1.4. Adult senescence, female pre-oviposition period, female fecundity and sex ratio. Adult senescence of both male and female of *B. dorsalis* was significantly affected by temperature. The Stinner function (Stinner et al., 1974) provided a good fit to the mean senescence vs temperature for male ($R^2 = 0.81$; P < 0.001; AIC = −12.80) and female ($R^2 = 0.84$; P < 0.001; AIC = −14.59) Table S4; (Fig. 4 a, b). The longevity of adults was significantly affected by temperature: males (F = 316.81; df = 5, 1359; P < 0.001), females (F = 375.80; df = 5, 1450; P < 0.001). As temperature increase, both male and female longevity decrease significantly (Table 4). The pre-oviposition period was also affected by temperature (F = 206.94; df = 4, 298; P < 0.001) as it decreased with increasing temperatures. The longest pre-oviposition period was observed at 15 °C (51.4 days) while the shortest period was observed at 30 °C (9.4 days) (Table 4). The relationship between total fecundity (mean total number of eggs laid per female throughout its lifespan) and temperature (F = 113.12; df = 4, 145; P < 0.001) was well described by the Wang 5 model ($R^2 = 0.99$; P = 0.009; AIC = 78.88) (Fig. 5; Table S4). The model predicted temperatures ranging between 20 and 30 °C to be favorable for high reproduction of the fly with a maximum fecundity at

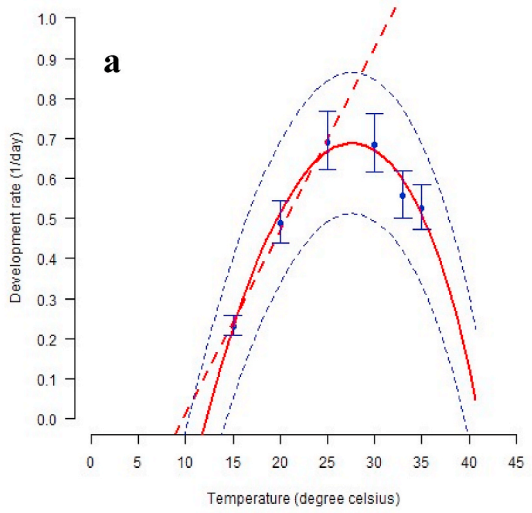
Table 2
Development time in days (mean ± SE) of *Bactrocera dorsalis* reared on 7 constant temperatures.

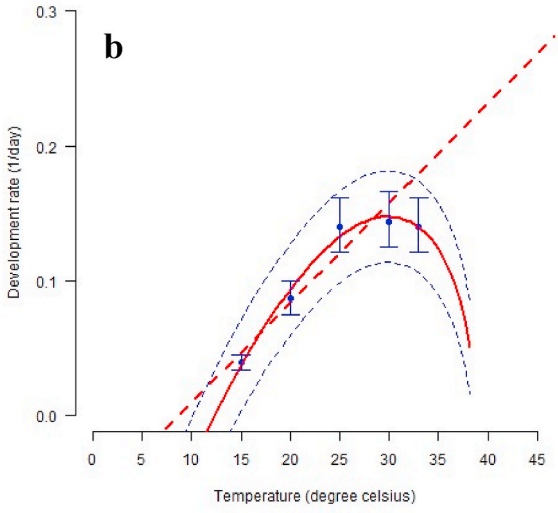
Temperature (°C)	Egg		Larva		Pupa		Egg to adult	
	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE	N	Mean ± SE
10	(3000)	–	–	–	–	–	–	
15	(3000)	4.31 ± 0.06a	(2177)	25.7 ± 0.42a	(286)	31.5 ± 0.32a	159	64.2 ± 0.91a
20	(3000)	2.50 ± 0.05b	(2429)	11.6 ± 0.20b	(1320)	14.3 ± 0.16b	1055	29.7 ± 0.35b
25	(3000)	2.01 ± 0.05c	(2638)	7.14 ± 0.12c	(1733)	9.02 ± 0.10c	1493	19.3 ± 0.17c
30	(3000)	1.46 ± 0.01d	(2516)	6.94 ± 0.12c	(1599)	7.51 ± 0.08d	885	16.3 ± 0.08d
33	(3000)	1.83 ± 0.04e	(2631)	7.14 ± 0.12c	(2045)	7.18 ± 0.09d	38	15.9 ± 0.21d
35	(3000)	1.92 ± 0.05e	(17)	-	-	-	-	-
F value		64.5		919.3		345.1		2110.9
df value		5		4		4		4
p value		<0.001		<0.001		<0.001		<0.001

Values followed by a different letter in the same column are significantly different using the Tukey's test. Number of individuals appears in parentheses. GLM *F*, *df*, and *p* values are presented at the end of the table for each life stage.

Table 3
Parameter estimates (±SEM) of the linear development model and predicted lower temperature thresholds and thermal requirements for each stage of *Bactrocera dorsalis*.

Stage	Parameters		R^2	F	Df	*P value*	Lower temperature threshold (°C)	Thermal requirements (Degree-Days)
	a	b						
Egg	0.032 ± 0.008	−0.241 ± 0.220	79.4	15.44	1, 4	0.017	7.53	31.25
Larva	0.004 ± 0.000	−0.025 ± 0.023	89.3	25.06	1, 3	0.015	6.25	250.00
Pupa	0.003 ± 0.000	−0.021 ± 0.007	96.2	76.67	1, 3	0.003	7.00	333





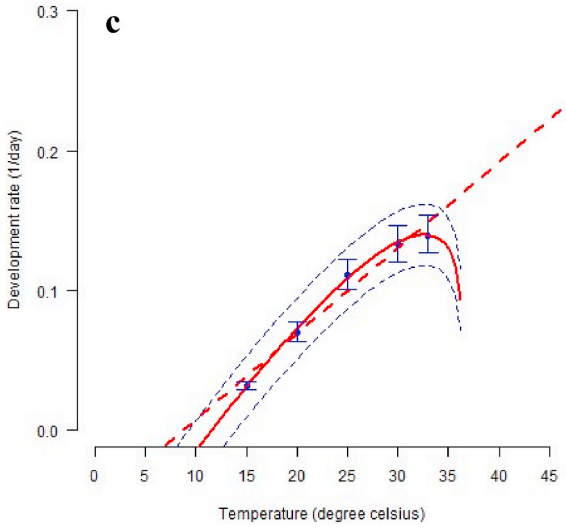
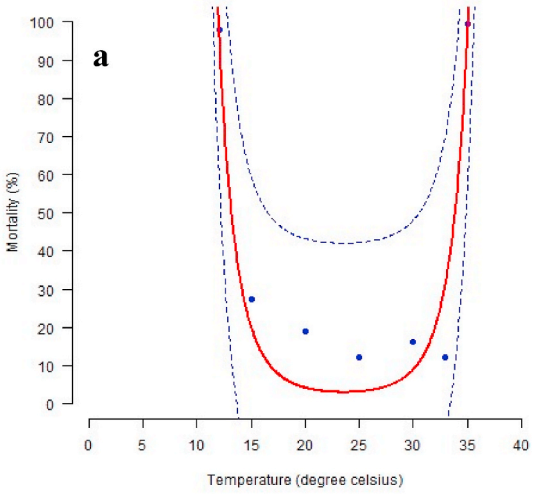
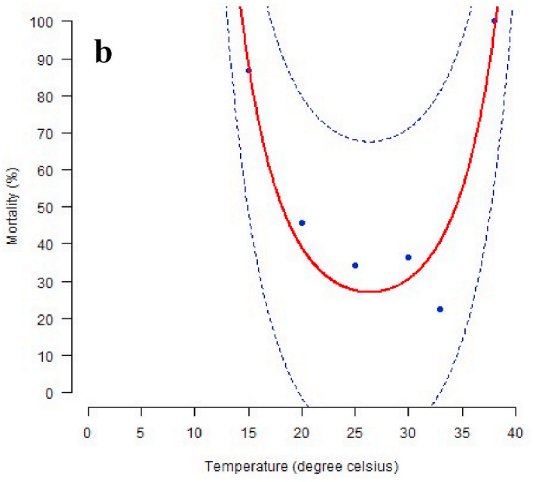


Fig. 2. a-c. Temperature-dependent developmental rate (1/d) for immature stages of *B. dorsalis*: (a) eggs (Briere 4 model), (b) larva (Briere 3 model), (c) pupa (Briere 4 model).





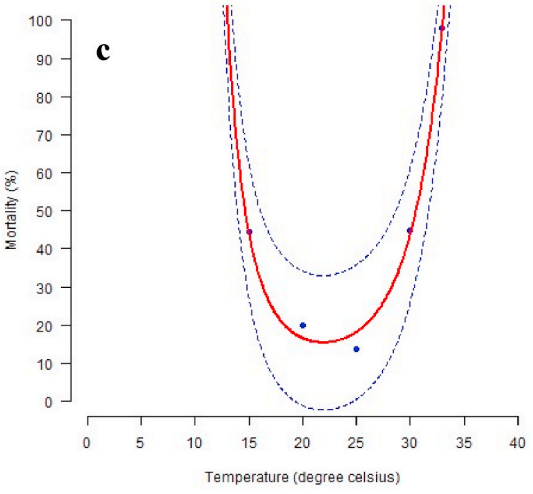


Fig. 3. a-c: Temperature-dependent mortality rates of immature life stages of *B. dorsalis*: (a) egg (Polynomial 2 model), (b) larva (Polynomial 2 model), (c) pupa (Polynomial 4 model); the upper and lower 95 % confidence intervals of the model are indicated with dotted lines; markers are observed lines.

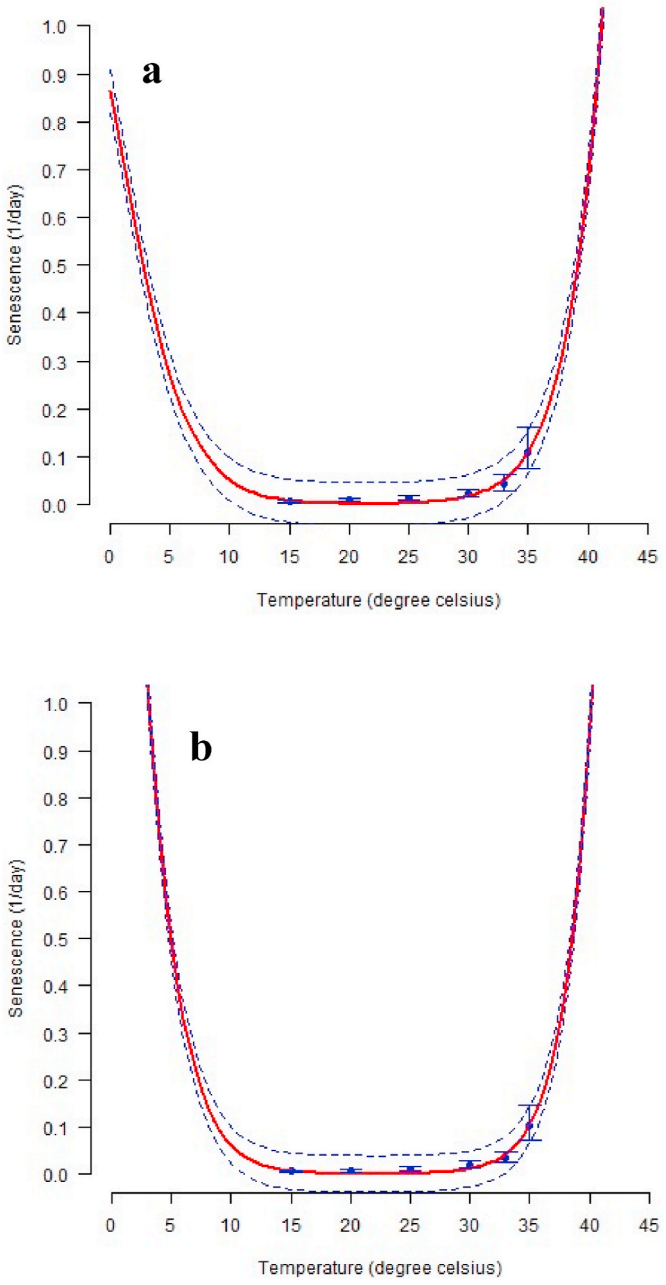


Fig. 4. a-b: Temperature-dependent senescence rates (1/d) for *B. dorsalis* adults: (a) male, (b) female. Fitted curves: Stinner 4 model; the upper and lower 95 % confidence intervals are indicated by dotted lines. Bars represent standard deviation of the mean.

25 °C. The Gamma model described the relationship between cumulative oviposition rate and female age (R^2 = 0.97; P < 0.001; AIC = −6366). 50 % of female's oviposition was completed by the time females reached a normalized age of 0.64 (Fig. 6; Table 4). There was no significant difference in the sex ratio at 20 °C (χ^2 = 273.40, df = 1, *P* = 0.506), 25 °C (χ^2 = 316.80, df = 1, *P* = 0.937) and 30 °C (χ^2 = 263.96, df = 1, *P* = 0.093). However, sex ratio was male-biased at 15 °C (χ^2 = 86.99, df = 1, *P* = 0.013) and female biased at 33 °C (χ^2 = 25.55, df = 1, *P* = 0.031) (Table 7).

2.5.1.5. Adult demographic parameters. All demographic parameters of *B. dorsalis* simulated at constant temperature are summarized in Table 5. Temperature significantly affected all estimated life table parameters. The intrinsic rate of natural increase (r_m) varied across temperatures (F = 255.10; df = 10, 100; P < 0.001) with highest values at 29 and 31 °C which was significantly different from the low values of 0.013 and 0.027 that were obtained at 15 and 19 °C respectively. Other parameters such as the gross reproductive rate (GRR) and the net reproductive rate (R_o) were also temperature-dependent with high values obtained between 23 and 29 °C for GRR (F = 40.81; df = 10, 100; P < 0.001) and the net reproductive rate R_o (F = 941.70; df = 10, 100; P < 0.001). The same trends were observed for other parameters: mean generation time (T) (F = 40.81; df = 10, 100; P < 0.001) and doubling time (D_t) (F = 52.90; df = 10, 100; P < 0.001), which decreased with increasing temperature; but the finite rate of increase (λ) (F = 263.20; df = 10, 100; P < 0.001) increased with increasing temperature.

2.5.1.6. Stochastic simulation at fluctuating temperatures and model validation. Stochastic simulation of the phenology model of *B. dorsalis* at fluctuating temperature Yaoundé, Cameroon) with an initial cohort of 100 eggs produced simulated demographic parameters presented in Table 6. From these results, *B. dorsalis* can complete its immature development within 20 days (addition of egg, larva and pupa development time), with a mortality rate of immature stages of 10, 35 and 54 % for egg, larva and pupa respectively. Globally, despite some differences observed between simulated and observed values, validation results showed similarities among demographic parameters such as the intrinsic rate of natural increase, the doubling time and the mean generation time (Table 6). The graphic representation of simulated and observed values for the life cycle is represented by Fig. 7.

3. Discussion

This study revealed that temperature exerts – as expected – an important influence on the development, survival and reproduction in *B. dorsalis* under laboratory conditions. Similar results have been obtained on *B. dorsalis* in other countries (Vargas et al., 1997; Rwomushana et al. 2009; Salum et al., 2014) and with other fruit fly species (e.g., Duyck and Quilici, 2002; Duyck et al., 2004a, b; Liu and Ye, 2009; Luo et al., 2009; Tanga et al., 2018; Choudhary et al., 2020). Within the temperature range used in our experiments (10–35 °C), increasing temperatures leads to faster development, low mortality rates for immatures stages and reproductive parameters. High temperatures (33 and 35 °C) however, showed the deleterious effects of heat observed on the phenology of *B. dorsalis*. Unlike previous studies, our study uses a modeling approach to investigate the role of wide range of constant and fluctuating temperature regimes to simulate the entire life cycle of the *B. dorsalis* including development and survival of immature stages and reproduction and longevity of adult males and females. As such, the present study provides greater insight into the role of temperature in the life history of *B. dorsalis* since its invasion of Africa, compared with other studies that restricted their investigations of the effects constant temperatures on either development rate and survival of immature stages (Rwomushana et al. 2009) or some demographic parameters at two constant temperatures (Salum et al. 2014). The results of these other studies cannot be used in the context of whole life cycle modeling, particularly for pest risk analysis.

Immature development was not observed at 10 and 35 °C, but at temperatures ranging between 20 and 30 °C, survival rate of all immature stages was at least 50% which may explain why *B. dorsalis* is widespread in the tropics where it experiences daily temperatures ranging between 20 and 30 °C and has not rapidly invaded regions where minimum and maximum temperatures exceeded the species temperature tolerance range. For example, *B. dorsalis* was recorded in 2018 in Italy, a country dominated by a Mediterranean climate (Nugnes et al., 2018); since then, the fly is present but is not yet well established as it was the case when it invaded tropical Africa. By the same token, Ekesi et al. (2006) reported that fruit infestation by *B. dorsalis* does not exceed 5 flies per Kg of mango in Kenyan highlands (>1500 masl) where

Table 4
Mean longevity, fecundity and pre-oviposition period of *Bactrocera dorsalis* at 6 constant temperatures in the laboratory.

Temperatures	N	Male longevity (days) Mean ± SE	N	Female longevity (days) Mean ± SE	N	Total Fecundity/female Mean ± SE	N	Pre-oviposition period (days) Mean ± SE
15	300	156.26 ± 4.631a	300	179.63 ± 5.51a	300	351.40 ± 35.90a	300	51.4 ± 2.7a
20	300	117.75 ± 4.23b	300	152.25 ± 4.41b	300	2120.60 ± 154.68b	300	17.9 ± 1.2b
25	300	70.75 ± 2.56c	300	81.85 ± 2.38c	300	2389.90 ± 116.20b	300	9.7 ± 0.4c
30	300	49.47 ± 1.56d	300	54.96 ± 1.62d	300	1122.93 ± 90.30c	300	9.4 ± 0.3c
33	300	25.18 ± 0.96e	300	30.6 ± 1.07e	300	75.43 ± 11.66a	300	14.4 ± 0.9b
35	300	9.38 ± 0.27f	300	9.66 ± 0.47f	300	–	300	–
F value		316.81		375.8		113.12		206.94
df value		5, 1359		5, 1450		4, 145		4, 298
p value		<0.001		<0.001		<0.001		<0.001

Values followed by a different letter in the same column are significantly different using the Tukey's test. Number of individuals appears in parentheses. GLM *F*, *df*, and *p* values are presented at the end of the table for each life stage.

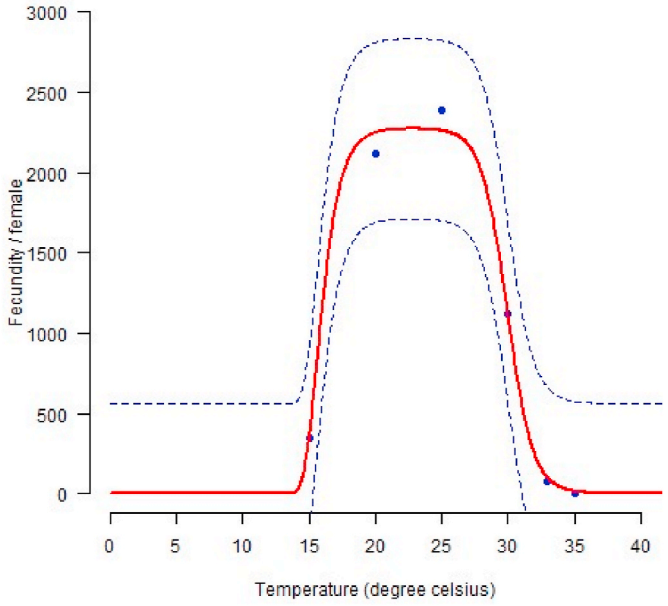


Fig. 5. Temperature dependent total oviposition curve; fitted curve: Wang 5 model.

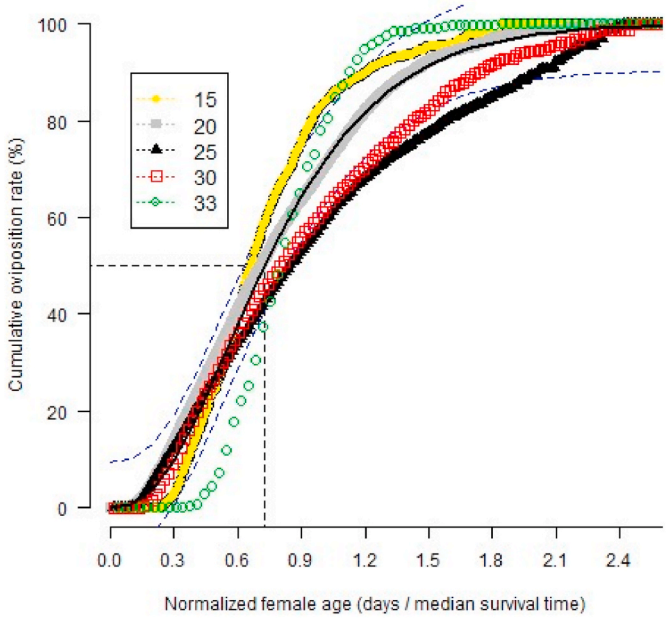


Fig. 6. Cumulative proportion of egg production in relation to *Bactrocera dorsalis* female age expressed as normalized time (senescence/mean senescence time). Data curves fitted with Gamma model.

average temperature is low compared to high average temperatures prevailing at low altitude (<500 masl), where established rapidly. Our results however are not fully consistent with previous findings on the life history of *B. dorsalis*. For instance, Rwomushana et al. (2009) in Kenya found that eggs and larvae developed at 35 °C but there was no adult emergence from pupae; while in China, *B. dorsalis* completed its whole development at 36 °C (Yang et al., 1994). These differences observed are common when working on the thermal response of insects from different strains. This might be explained by a combination of adaptation to local climate and thermal plasticity in insect populations when exposed to different climatic conditions for laboratory experiments (Pieterse et al., 2017; Motswagole et al., 2019), or differences in experimental set-up and insect handling. We also found that high temperatures were deleterious to the emergence of adults from pupae. At 33 °C for instance, 98 % of pupae were empty or contained dead flies, suggesting that at this temperature, immature development was accelerated leading to the non-maturity of subsequent individuals. This is very important result because in practice, pupation occurs in the ground. The temperature of the soil is then one of the determinants for successful emergence of the flies. This aspect of life cycle of *B. dorsalis* is important to be well understood as it may have considerable effect on overall population dynamics of the fly especially in the Sahelian zone where temperatures are generally high throughout the year.

Models are important tools that can be used to describe the response of an insect's development and reproduction under variable environmental conditions. In the present study, the development rate of *B. dorsalis* was assessed at constant temperatures and modeled using linear and non-linear approaches. Linear models have been commonly used to describe the relationship between temperature and the development rate of immature stages of insects with the assumption that after the lower threshold temperature, the development rate is linear and become non-linear at high temperature (Wagner et al., 1984; Worner, 1992). The linear model applied on the development rate of immature stages of *B. dorsalis* has shown that the linearity was observed between 15 and 25 °C for eggs, 15 and 30 °C for larvae and pupae. Moreover, the linear regression revealed that the correlation coefficient was close to 1.0, confirming the strong linearity of the development rate of immature stages between 15 and 30 °C. From the linear regression, we estimated the total thermal constant at 614.58 DD and the lower threshold temperature of 7.53, 6.25 and 7.00 °C for egg, larva and pupa respectively. Our results contrasted with those of Rwomushana et al. (2009) who assessed the development of immature stages of *B. dorsalis* in Kenya and obtained a linear relationship between 15 and 35 °C for egg and larvae while in our case, the linearity was not respected between 30 and 33 °C.

Table 5
Simulated life table parameters of *Bactrocera dorsalis* at 11 constant temperatures.

Temperature (°C)	Parameters					
	r_m	GRR	R_o	T	λ	D_t
15	0.013 ± 0.001a	150.83 ± 30.43a	3.80 ± 0.68a	124.80 ± 5.50a	1.009 ± 0.001a	72.35 ± 6.21a
17	0.027 ± 0.001bc	288.30 ± 31.64bcd	49.74 ± 7.70a	141.30 ± 2.50b	1.027 ± 0.001bc	26.22 ± 1.27bc
19	0.027 ± 0.000bc	300.55 ± 14.13cd	113.85 ± 6.90b	175.41 ± 0.10c	1.027 ± 0.000bc	25.82 ± 0.45bc
21	0.024 ± 0.000c	223.94 ± 18.61abc	104.08 ± 8.08b	195.40 ± 1.21d	1.023 ± 0.000b	29.50 ± 0.76b
23	0.030 ± 0.000bc	352.90 ± 26.49de	177.91 ± 13.27cd	170.30 ± 0.70c	1.030 ± 0.000bc	22.98 ± 0.50bc
25	0.048 ± 0.000d	648.80 ± 26.97f	326.60 ± 21.12e	119.12 ± 0.70a	1.050 ± 0.000d	14.34 ± 0.20cd
27	0.074 ± 0.001e	1163.17 ± 46.84f	229.33 ± 19.79f	72.85 ± 0.42e	1.077 ± 0.001e	9.37 ± 0.19d
29	0.102 ± 0.001f	1079.46 ± 54.78e	134.78 ± 9.29bc	48.06 ± 0.40f	1.107 ± 0.001f	6.84 ± 0.12d
31	0.102 ± 0.002f	368.24 ± 18.35abc	34.74 ± 3.38a	34.20 ± 0.42g	1.107 ± 0.002f	6.80 ± 0.13d
33	0.035 ± 0.005h	176.33 ± 28.02 ab	2.76 ± 0.42a	25.72 ± 0.70g	1.036 ± 0.005c	25.76 ± 5.25bc
35	–	–	–	–	–	–
F	255.10	40.81	85.30	941.70	263.20	52.90
Df	10, 100	10, 100	10, 100	10, 100	10, 100	10, 100
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Values followed by a different letter in the same column are significantly different using the Tukey HSD test ($P < 0.05$). Number in parentheses are standard error. ANOVA *F*, *df*, and *p* values are presented for each life stage. r_m, intrinsic rate of natural increase; R_o, Net reproductive rate (Females/female/generation); T, mean generation time (days); λ, finite increase rate (Female/female/day); D_t, doubling time (days).

Table 6
Validation between observed and simulated life table parameters of *B. dorsalis* using fluctuating temperatures prevailing in Yaoundé-Cameroon during the year 2013.

Parameters	Observed	Simulated values	*p*
Development time (days)			
Egg	2.10	1.79 ± 0.08	0.001
Larva	11.93	8.06 ± 0.31	0.000
Pupa	11.50	10.91 ± 0.17	0.045
Mortality (%)			
Egg	0.28	0.10 ± 0.04	0.000
Larva	0.44	0.35 ± 0.08	0.003
Pupa	0.52	0.54 ± 0.09	0.370
Life history parameters			
Intrinsic rate of natural increase (r_m)	0.09	0.09 ± 0.01	0.050
Net reproductive rate (R_o)	815.44	427.12 ± 40.73	0.000
Gross reproductive rate (GRR)	1733.10	1304.53 ± 78.25	0.000
Mean generation time (T)	76.02	63.20 ± 3.00	0.000
Finite rate of increase (λ)	1.09	1.09 ± 0.01	0.515
Doubling time (Dt)	7.86	8.08 ± 1.17	0.370

Table 7
Effect of 6 constant temperatures on sex ratio of *Bactrocera dorsalis*.

Temperatures (°C)	Sex ratio (%)		Statistics		
	Male	Female	χ^2	df	*P*
15	51.08a	48.92b	86.99	1	0.013
20	50.67a	49.33a	273.40	1	0.506
25	49.41a	50.59a	316.80	1	0.937
30	48.45a	51.55a	263.96	1	0.093
33	37.84a	62.16b	25.55	1	0.031

Means followed by the same letter in the same row are not significantly different by the χ^2 test, $P < 0.05$.

This result suggests that the thermal tolerance breath for the immature development of our population is narrower compared with that of the Kenyan population which might indicate that the latter population can easily adapt or invade areas dominated with high temperatures. Also, while we obtained lower threshold temperatures of 7.53, 6.25 and 7.00 °C for the egg, larva and pupa respectively and a total thermal constant of 614 DD, Rwomushana et al. (2009) estimated the total thermal constant of 377 DD and the lower threshold temperature of 8.8, 9.4 and 8.7 °C for egg, larva and pupa respectively. Similarly, Vargas et al. (1997) examined *B. dorsalis* in Hawaii at temperature ranging from 16 to 32 °C and obtained a total thermal constant of 358 DD and the threshold temperature was 11.8, 5.6 and 9.3 °C for egg, larva and pupa

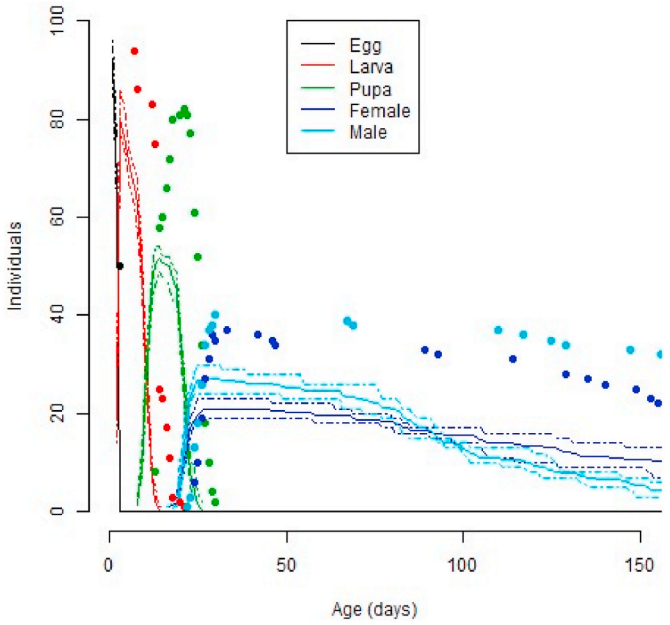


Fig. 7. Observed and simulated life table values for *B. dorsalis* displayed on the validation graph. Dots represent observed values obtained from fluctuated temperatures and lines are those from simulated model. Solid lines are averages of the simulations while the broken ones indicate the minimum and maximum values obtained from simulations.

respectively. These differences might be explained by the fact that populations of *B. dorsalis* used for these studies are from different strains and occur in environment with different climate profiles, or by possibly other factors related to insect handling and experimental setup. For example, the strains used by Vargas et al. (1996) and Rwomushana et al. (2009) were from a colony kept in the laboratory for about 300 and 100 generations respectively while ours was only maintained for three generations in the laboratory. Further, it suggests high plasticity in immature development of *B. dorsalis* to different thermal environments which is likely one of the reasons the fly successfully invaded many countries in a short period of time. Also, the diet (wheat-based for Vargas et al. (1996) and carrot-based for Rwomushana et al. (2009) used to feed larvae could have played a role in the development time of immature stages and hence on the determination of threshold temperature and thermal constant. The determination of the lower threshold

temperature and the thermal constant are important since they are limiting factors in the establishment and the invasion of a species in a new geographical area (Andrewartha and Birch, 1954; Bursell, 1964). The development rate of immature stages at 33 °C decreases and the linearity with other temperatures was not respected, suggesting that high temperatures can slow development rate. This portion was then predicted using non-linear models and suggests that the optimal development temperature is between 25 and 33 °C and the upper threshold is between 33 and 35 °C. To our knowledge, this study is the first to predict the development rate of immature stages of *B. dorsalis* using non-linear models allowing to better understand the phenology of the pest when exposed at high temperatures. This is particularly important because in the natural environment, these insects can experience temperature above 35 °C but their survival will depend on the duration of exposure and the heterogeneity of the habitat (Bonebrake and Deutsch, 2012).

Our findings on adult longevity and female pre-oviposition period of *B. dorsalis* revealed that these parameters were prolonged at low temperatures and gradually decreased with increasing temperature but surprisingly, the pre-oviposition period was prolonged at 33 °C compared with 30 °C. The longer pre-oviposition period at 33 °C suggests deleterious effects of high temperatures on the physiology of the insect. The pre-oviposition period and adult's longevity of *B. dorsalis* have been estimated at different temperature ranges in Hawaii by Vargas et al. (1997), in Tanzania by Salum et al. (2014) and in China by Yang et al. (1994). Though the temperature scales used by the three authors were not the same as ours, values obtained at similar temperature levels were not the same. For instance, we obtained pre-oviposition period of 51.4, 9.7, 9.4 and 14.4 days at 15, 25, 30 and 33 °C respectively while Vargas et al. (1997) obtained 31.8, 7.3, 5.7 and 5.3 days at 16, 24, 29 and 32 °C respectively. Yang et al. (1994) obtained 13, 17 and 15 days at 25, 31 and 34 °C respectively while Salum et al. (2014) obtained a pre-oviposition time of 11 days at 25 °C. As for pre-oviposition period, adult's longevity period varied with temperatures, with higher longevities at low temperatures while at high temperature (33 and 35 °C), harmful effect of long exposure to heat was observed with adult flies not able to spend 10 days at 35 °C. Our results were different from those of Vargas et al. (1997) though longevity was prolonged at low temperatures (up to 133 and 116 days for males and females respectively at 16 °C while we obtained a longevity of 179 and 156 for females and males respectively at 15 °C.

We found a low total fecundity at 15 °C, very high at temperatures ranging between 20 and 30 °C, followed by drastic decrease at 33 °C, with no reproduction at 35 °C. The decline in fecundity at 33 °C and the absence of reproduction at 35 °C reflect two important aspects of the physiology of the fly and its thermal performance: 1) high temperature leads to high adults' mortality and affect the maturity of ovaries of females and the spermatophores of males and 2) the lethal temperature of *B. dorsalis* lies between 33 and 35 °C under laboratory conditions. Adult demography parameters followed the same trend with important variation obtained with increasing temperatures. Our results show high reproductive potential of *B. dorsalis* within the eleven temperatures chosen for stochastic simulations. The fly shows important reproductive potential even at low constant temperature. At temperature ranging between 15 and 21 °C for instance, *B. dorsalis* has an intrinsic rate of natural increase up to 2.7 %, a gross reproductive rate can reach 300 eggs and a long lifespan. These results contrasted with those of Vargas et al. (1997) who found a negative intrinsic rate of natural increase (−0.0003 at 16 °C and −0.137 at 32 °C) and relatively low net reproductive rate (1.5 at 16 °C and 0.2 at 32 °C). Also, our intrinsic rate of increase at 25 °C ($r_m = 0.048$ %) and 31 °C (0.102 %) were far different from that of Salum et al. (2014) at 25 °C ($r_m = 0.128$ %) and 30 °C. The cause of these differences is not clear but, experimental set-up (egg laying device, rearing diet etc.) and the strain of the fly cannot be disregarded. Also, while we have used the model built in the ILCYM software to stochastically simulate the life table parameters of the fly at each temperature, Salum et al. (2014) and Vargas et al. (1997) rather used the deterministic demographic formula developed by Carey et al. (1993). The optimal reproductive parameters (r_m, GRR, R_o, T, λ and D_t) obtained from our stochastic simulations combined with optimal development rate and low mortality for immature stages were found at temperatures ranging between 25 and 31 °C. In this temperature range, one can find the mean annual temperature of many tropical locations, and hence explain the rapid invasion of these areas by *B. dorsalis*.

The phenology model developed under constant temperature was validated in our study using fluctuating temperatures recorded in the town of Yaoundé during the year 2013 and results revealed that *B. dorsalis* still has high demographic potential despite temperature variation. Similarities were obtained between observed and simulated demographic parameters such as the intrinsic rate of natural increase, the finite rate of increase and the doubling time, meaning that our phenology model is good in predicting the development and reproduction of *B. dorsalis*. Differences noted between simulated and observed in other parameters such as R_o, GRR and T; these differences can be attribute to deviances observed in the model, a situation which is common in modeling (Fand et al., 2014).

The sex ratio of *B. dorsalis* was balanced between 20 and 30 °C while it was male-biased at 15 °C and female biased at 33 °C. To our knowledge, no study has explored the effect of temperature on the sex ratio of *B. dorsalis*. This study thus provides new insight regarding the effect of temperature on the sex ratio of *B. dorsalis*. Sex ratio is an important parameter when studying the life table of insects (Carey and Roach, 2020). In tephritids for instance, females are responsible for the damage caused to their host through egg deposition in the fruit and subsequent larval development that can destroy the fruit depending on infestation level. A female-biased population can create more damage than a male-biased population and can naturally contribute to higher population growth rate.

The overall life table of *B. dorsalis* in this study demonstrates the competitive abilities of this species to displace the native *Ceratitis* species (Ekesi et al., 2009) and its rapid spread over the African continent and especially in tropical zones. The reproductive activity at constant low temperature was quite high and might also explain the current colonization of temperate regions by the pest (Nugnes et al., 2018; Papadopoulos et al., 2013; Suckling et al., 2014). However, laboratory conditions are obviously different from ecological conditions prevailing in the natural environment which can have deep impact regarding our findings. Similar study conducted under natural or semi-natural conditions will contribute more knowledge development and reproduction of the insect and will help to understand the population dynamics of *B. dorsalis*. Hence, demographic parameters obtained in this study suggest that population dynamics of *B. dorsalis* might be different depending on the climate prevailing in each locality. All these phenological performances are closely linked with the quality and quantity of host plants which are key element in the invasiveness ability of many insect pest species (Leblanc et al., 2013).

In the framework of *B. dorsalis* management in several regions of the world, the endoparasitoid *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae) has been shown to be the effective parasitoid in the control *B. dorsalis* population (Mohamed et al. 2010; Vargas et al. 2007, 2012, 2013; Gnanvossou et al., 2017). Recent studies provided evidence from Africa for the establishment and impact of *F. arisanus* on *B. dorsalis* (see Gnanvossou et al., 2017). Other studies have also shown that the lower and upper thermal thresholds for two *F. arisanus* populations are 6.9–10.1 °C and 33.7–34.8 °C respectively in Cameroon (Nanga Nanga et al., unpublished data) and Kenya (Appiah et al., 2013). These thresholds are within the ranges of those for *B. dorsalis* (this and other studies) which provide further support for the ability of *F. arisanus* to persist in environments that are also favorable to its host. Additional modeling of the effect of climate on both *B. dorsalis* and *F. arisanus* at both local and global levels are needed however to provide further knowledge and the overlap in distribution and abundance of the pest and its natural enemies.

The present study has demonstrated the role of temperature in shaping some phenological characteristics of the oriental fruit fly *B. dorsalis* using a modeling approach. The results from our study will contribute to the understanding the role of warming climate in the invasion, the population dynamics and the ecology of this pest. Similar studies in which the development and reproduction of this pest under fluctuating temperature from different agro-ecologies are needed to validate our findings from the laboratory. It is also an important step towards the development and implementation of an integrated pest management strategy for the regional control of this pest.

CRediT authorship contribution statement

Dongmo K. Michel A.: Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Komi K.M. Fiaboe:** Validation, Formal analysis, Writing – review & editing, Supervision. **Sévilor Kekeunou:** Conceptualization, Formal analysis, Writing – review & editing, Supervision. **Samuel N. Nanga:** Methodology, Data curation, Writing – review & editing. **Apollin F. Kuate:** Methodology, Data curation, Writing – review & editing. **Henri E.Z. Tonnang:** Conceptualization, Methodology, Validation, Resources, Writing – review & editing. **Désiré Gnanvossou:** Methodology, Writing – review & editing. **Rachid Hanna:** Conceptualization, Formal analysis, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2021.102877.

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