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**Author for correspondence:**
R. Babin,
Email: regis.babin@cirad.fr

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# Temperature-dependent development and survival of immature stages of the coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae)

A.G.A. Azrag[1,2,3], A.A. Yusuf[2], C.W.W. Pirk[2], S. Niassy[1], K.K. Mbugua[1] and R. Babin[1,4,5]

[1]International Centre of Insect Physiology and Ecology, P.O. Box 30772-00100, Nairobi, Kenya; [2]Department of Zoology and Entomology, Social Insect Research Group, University of Pretoria, Private Bag X20, Hatfield, Pretoria 0028, South Africa; [3]Department of Crop Protection, Faculty of Agricultural Sciences, University of Gezira, P.O. Box 20, Wad Medani, Sudan; [4]CIRAD, UPR Bioagresseurs, P.O. Box 30677-00100, Nairobi, Kenya and [5]Bioagresseurs, Univ Montpellier, CIRAD, Montpellier, France

### Abstract

Although the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae) is the most destructive insect pest of coffee worldwide, there is much to learn about its thermal biology. This study aimed to develop temperature-based models for *H. hampei* development and to provide the thermal requirements of immature stages in the laboratory. Using a new observation method, larval development and survival were monitored daily on fresh Arabica coffee seeds, under seven constant temperatures in the range 15–35°C, with 80 ± 5% RH and 12:12 L:D photoperiod. Linear and non-linear functions were fitted to the development data plotted against temperature, using Insect Life Cycle Modelling software (ILCYM). Temperature significantly affected the development time of all immature stages. Egg incubation period ranged 4.6–16.8 days, under temperature between 30 and 15°C. No development occurred at 35°C and the larval stage did not develop to pupa at 15°C. The minimum temperature threshold ($T_{\min}$) estimated from linear regression was 10.5, 13.0, 15.0 and 13.0°C, for egg, larva, pupa and the total development from egg to adult, respectively. The maximum temperature threshold ($T_{\max}$) estimated from the Sharpe and DeMichele function was 32°C for egg to adult development. The thermal constant ($k$) was estimated at 78.1, 188.7, 36.5 and 312.5 degree days, for egg, larva, pupa and for egg to adult, respectively. Our results will help understand and predict the pest population dynamics and distribution in coffee plantations as impacted by temperature, and as such, will contribute to a more efficient management of the pest.

## Introduction

Predicting the risk of an insect pest outbreak largely contributes to a more efficient management strategy. Prevision of pest population dynamics helps implement well-prepared and better-targeted control measures. In many cases, pest outbreaks are initially due to relatively small numbers of individuals colonizing the crop. These individuals find optimal conditions for their development and quickly reach high population levels threatening the crop. Knowing these optimal conditions and their impact on population dynamics is therefore critical to prevent an outbreak. As poikilotherm animals, insects depend primarily on the temperature of their environment to develop (Régnière *et al.*, 2012). Pest distribution and population dynamics, therefore, can be largely predicted by running temperature-dependent models of development (Tonnang *et al.*, 2013; Azrag *et al.*, 2018). These tools also provide standard life history traits such as temperature thresholds and thermal constant that characterize the relationships between insect development and temperature (Wagner *et al.*, 1991; Nielsen *et al.*, 2008; Azrag *et al.*, 2017).

Although the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae) is the most devastating insect pest of coffee worldwide (Damon, 2000; Jaramillo *et al.*, 2006; Vega *et al.*, 2009), there is much to learn about its thermal biology. This tiny and discreet beetle feeds on coffee berries at all maturation stages, leading to losses of both quantity and quality of coffee beans (Le Pelley, 1968; Vega *et al.*, 2003; Jaramillo *et al.*, 2010). Feeding damage is of two types: adult female feeding lesions on developing fruits lead to berry drop, and offspring feeding galleries in the berry endosperm (coffee seeds) lead to bean weight loss and increased vulnerability to disease infection. Economic losses due to *H. hampei* infestations globally are estimated at US$500 million

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annually (Pardey, 2015). In eastern Africa, infestation level can be as high as 80–90% in medium to low-elevation coffee plantations (<1500 m asl), causing serious economic loss to the predominant small scale farmers (Jonsson *et al.*, 2015).

Life history traits such as high reproductive rate and short life cycle (Jaramillo *et al.*, 2009) may account for the success of *H. hampei* as a devastating pest of coffee. Another factor is that *H. hampei* spends most of its life cycle inside the coffee berry that makes damage difficult to detect at first sight, and chemical spraying usually inefficient (Brun *et al.*, 1989). Biological and semiochemical control attempts have shown some success (Damon, 2000; Dufour & Frérot, 2008). In spite of this, until now, none of the control methods recommended for the control of *H. hampei* has achieved the complete eradication of the pest. Rather, new areas of Arabica coffee production are under increasing threat due to global warming (Jaramillo *et al.*, 2009; 2011). Thus, it becomes urgent to develop new tools and knowledge to support existing management strategies for the pest.

Literature dealing with *H. hampei* biology reports inconsistent data on pest development as influenced by temperature. For example, Barrera (1994) reported a larval development time of 17 days at 27°C, while it was 13 days at the same temperature in the study by Fernández & Cordero (2007). The reason for this may be the use of different methodologies for rearing and observation. *H. hampei* life cycle inside coffee berries makes direct observation difficult and berry dissection may be a source of disturbance that may lead to assessment bias. A first output of the present study is a new rearing and observation method that overcomes this difficulty. This method allowed the monitoring of the development of *H. hampei* immature stages on a daily basis under seven constant temperatures in the laboratory. This paper therefore provides basic data for *H. hampei* immature stage development as influenced by temperature. The third output of this paper is a set of standard temperature-dependent models of development that characterize the relationship between *H. hampei* development and temperature and provide thermal requirements of this major pest of coffee. As components of a general phenology model for *H. hampei*, these models will help predict the distribution of *H. hampei* as influenced by temperature on coffee, in the context of global warming.

## Materials and methods

### Insect field collection for colony initiation

Experiments started with the collection of *H. hampei* adult females from field populations. Initial sampling was done in small holding coffee farms located on the Aberdare range, in Murang'a County, Kenya (sampling area between 0.710°S, 37.083°E and 0.695°S, 36.923°E, with elevation range ≈1300–1800 m asl). In this area, annual rainfall ranges ≈1200–1800 mm, with two rainy seasons, from mid-March to May and from October to mid-December, the former being the most important (Ovuka & Lindqvist, 2000). The annual mean temperature varies according to elevation, with ≈20°C at 1500 m asl. In the area, land use is dominated by small scale coffee farms, mixed with food crops such as maize, beans and banana, with trees such as grevillea, *Grevillea robusta* A. Cunn. ex R. Br. and macadamia, *Macadamia* spp. that provide shade to coffee trees. Coffee berries infested by *H. hampei* were collected from 13 coffee farms. Infested berries are easily detected by the holes the females drill, almost always at the apex of the berry, to penetrate the fruit. Berries were kept in 0.5-litre plastic containers (Foodmate, Kenpoly Manufacturers Ltd, Kenya), measuring 10.4 cm in mean diameter and 6 cm deep, for transportation to the coffee pest laboratory at International Centre of Insect Physiology and Ecology (*icipe*), Kenya. Container lids had a 4 cm diameter opening, covered with a fine mesh tissue for aeration. Enough infested berries were collected to fill 20 of these containers. In the laboratory, the containers were kept for three weeks in an incubator (SANYO MIR-553, Sanyo Electrical Ltd, Tokyo, Japan) set at 25 ± 0.5°C, with 80 ± 5% RH and 12:12 L:D photoperiod (Jaramillo *et al.*, 2010). Afterwards, the berries were dissected with a scalpel under a stereo microscope using the ×10 magnification and females were gently collected with a mouth aspirator. Approximately 12,000 *H. hampei* adult females were collected this way for subsequent experiments.

### Egg production

Mature berries of *Coffea arabica* var. Ruiru 11 were collected from the same coffee farms where *H. hampei* were sampled for colony initiation. The berries were carefully checked for infestation and only non-infested fruits were collected and transported to the laboratory. Here, berries were washed with detergent (Teepol, Sudi Chemical Industry Ltd, Kenya), then thoroughly rinsed with water and finally placed on a paper towel for 2 h to dry at room temperature. Afterwards, the berries were distributed in 60 containers of the same type as those used for field collection (0.5-litre aerated plastic containers), with each container containing 80 berries. Then, approximately 200 reproductive *H. hampei* females obtained from field-collected infested berries were introduced into each container. After 18 h, newly infested berries were collected and transferred into new containers (each container had between 50 and 70 infested berries) of the same type as previously (0.5-litre aerated plastic containers) but, lined with a humidified mixture of plaster of Paris and activated charcoal to maintain a high level of humidity (Jaramillo *et al.*, 2010). These containers were incubated (as previously described) at 25 ± 0.5°C, with 80 ± 5% RH and 12:12 L:D photoperiod. Five days after infestation, the berries were dissected under a stereo microscope using the ×10 magnification and the eggs were carefully collected using a fine camel-hair brush and placed on discs made of paper towels in small plastic Petri dishes (3.5 cm wide, 1 cm deep). Each Petri dish contained 10–12 eggs to ease observation under the stereo microscope. We assumed that most of the eggs were ≤24 h old at that time (all of them were <48 h), since *H. hampei* females usually start laying eggs 4–6 days after they have penetrated the berry (Jaramillo *et al.*, 2010).

### Development and survival of immature stages

Eggs obtained with the method described above were incubated in laboratory incubators of the same model as previously mentioned, but now set at the following seven constant temperatures: 15, 18, 20, 23, 25, 30 and 35°C (± 0.5°C), with 80 ± 5% RH and 12:12 L:D photoperiod. For each temperature, between 100 and 200 eggs were observed daily for a month under a stereo microscope (×10 magnification) to detect hatching and assess the incubation period. The eggs that did not hatch during this period were observed for two additional weeks and then, if not hatched, recorded as dead.

After emerging, the larvae were reared individually on fresh coffee seeds. Mature coffee berries were dissected to extract the

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two seeds from inside. Then, a slit approximately 1.5 mm deep and 2 mm wide was dug on the seed using a sharp scalpel blade, where the larva was carefully placed using a fine camel hair brush. The seed with the larva was gently wrapped with aluminium foil to maintain the larva in conditions as close as possible to those inside the berry and to prevent the larva from escaping. Each seed with larva was labelled and placed in a well (2.5 cm in diameter and 2 cm deep) of a 12-well plate (Costar, Corning Inc., NY, USA). Larvae were transferred to new fresh seeds every 4 days to prevent them from boring deeply in the seed. The larvae were monitored daily under a stereo microscope to record the pupation and mortality. After pupation, the pupae were carefully extracted from the seeds and kept in the same well plates lined with paper towel and monitored daily until adults emerge. This rearing method enabled us to directly observe the development and survival of all immature stages and follow the same individuals from egg to adult.

## Model parameterization

The impact of temperature on the development and mortality of *H. hampei* immature stages was described with linear and non-linear functions using the Insect Life Cycle Modelling software (ILCYM, version 3.0) (Tonnang *et al*., 2013). ILCYM includes a model builder that facilitates the fitting of non-linear functions to the observed data. These models allow the calculation of the thermal requirements of the insect by describing the temperature dependency of development time, development rate and mortality rate for each life stage. The best-fitted models were selected based on their coefficient of determination ($R^2$) and Akaike's information criterion (AIC) (Tonnang *et al*., 2013).

### Modelling the development time distribution

The frequency distributions of insect development time are usually skewed, and it is assumed that the distributions have the same shape at different constant temperatures (Sharpe & DeMichele, 1977). In a first step, cumulative frequencies of development times were plotted, for each life stage and temperature, against ln-transformed development times (normalized development time). Then, common binary distribution models were fitted to observed data in a parallel line approach to estimate the development time. The estimated development time was the median of the distribution; in other words, the time required for 50% cumulative frequency of individuals in each life stage to complete the development. The best-fitted models were complementary log–log (CLL) model for the egg stage and the complete development from egg to adult, and probit model for the larva and pupa stages. The mathematical expressions of the CLL and probit functions are given in table 2 (Tonnang *et al*., 2013).

### Modelling the effect of temperature on the development rate

The development rate was calculated at each constant temperature and for each immature stage, and for the complete development from egg to adult as the inverse of the median development time (development rate = 1/development time). We chose median development time because distributions of insect development time usually have similar shapes and the use of median in this case yields one standard curve for all temperatures (Wagner *et al*., 1984). In addition, the median is less sensitive to outliers compared to the mean times, especially when the distribution of the development is skewed to the longer times (Wagner *et al*., 1984). The calculated development rate was plotted against temperature and fitted to linear models following the formula:

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

where $r(T)$ is the development rate at temperature $T$; $a$ is the intercept and $b$ is the slope of the regression line. The minimum temperature threshold ($T_{\min}$), at which the development rate = 0, was estimated using the intercept and slope of the regression line: $T_{\min} = -a/b$; while the thermal constant $k$ (in degree days) was estimated using $k = 1/b$.

In our study, the relationship between development rate and temperature fitted well to linear regressions for all temperatures. However, this relationship is usually not linear for the highest temperatures of development as demonstrated for other insect species (Sharpe & DeMichele, 1977). Therefore, non-linear models were also used to describe this effect for each immature stage. In addition, non-linear models allow the assessment of the maximum temperature threshold ($T_{\max}$). The Logan model (Logan *et al*., 1976) predicted well the effect of temperature on development rates for egg and pupa stages, while the modified version (five parameters) of the biophysical Sharpe and DeMichele model (Sharpe & DeMichele, 1977) gave the best fit to the larval stage and for the period from egg to adult. The mathematical expressions of the models are presented in table 4 (Tonnang *et al*., 2013).

### Modelling the effect of temperature on the mortality rate

Mortality rate was calculated for each life stage at given temperatures from the number of surviving individuals. Then, a modified version of the Wang model (Wang *et al*., 1982) was applied to describe the effect of temperature on the mortality rate of each immature stage, while a second-order polynomial function was used for the mortality rate for the period from egg to adult. The mathematical expressions of these models are presented in table 5 (Tonnang *et al*., 2013).

## Statistical analyses

The effect of temperature on *H. hampei* developmental time (in days) was assessed for each development stage and for the complete development from egg to adult. Data for egg incubation period, larva and pupa development time, and egg to adult development were separately subjected to generalized linear model (GLM) with a Poisson distribution as recommended by O'Hara & Kotze (2010). R programming environment (R Core Team, 2016) was used for calculations with temperature as an independent variable. Once significant differences were detected, data were submitted to post hoc analysis for mean comparison using Tukey's test at $\alpha = 0.05$.

# Results

## Development time

Development occurred between 15 and 30°C for egg and between 18 and 30°C for larva and pupa (table 1). The impact of temperature on the observed development times was significant for every *H. hampei* immature stages, as well as for the complete development time from egg to adult (egg: $\chi^2 = 436$, $df = 848$, $P < 0.0001$; larva: $\chi^2 = 416.9$, $df = 745$, $P < 0.0001$; pupa: $\chi^2 = 317.98$, $df = 920$, $P < 0.0001$; egg to adult: $\chi^2 = 106.26$, $df = 81$, $P < 0.0001$). The mean observed development time for egg ranged between

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**Table 1.** Observed mean development time and development time simulated from the models (median of the distribution) for immature stages of *H. hampei* reared in the laboratory at different constant temperatures.

| | | Egg | | Larva | | Pupa | | Egg to adult | |
|---|---|---|---|---|---|---|---|---|---|
| *T* (°C) | *n* | Observed | Simulated | Observed | Simulated | Observed | Simulated | Observed | Simulated |
| 15 | 112 | 16.86 ± 0.46a | 16.83 ± 0.38a | – | – | – | – | – | – |
| 18 | 200 | 11.58 ± 0.18b | 11.09 ± 0.28b | 39.45 ± 0.55a | 38.34 ± 0.54a | 13.58 ± 0.26a | 12.71 ± 0.28a | 63.38 ± 0.76a | 62.79 ± 0.79a |
| 20 | 167 | 8.93 ± 0.16c | 8.55 ± 0.18c | 29.12 ± 0.28b | 28.26 ± 0.39b | 7.29 ± 0.11b | 6.57 ± 0.20b | 46.75 ± 0.32b | 44.19 ± 0.50b |
| 23 | 161 | 6.57 ± 0.11d | 6.12 ± 0.14d | 21.09 ± 0.23c | 20.32 ± 0.30c | 5.80 ± 0.10c | 5.01 ± 0.12c | 33.71 ± 0.21c | 32.82 ± 0.42c |
| 25 | 191 | 5.76 ± 0.10e | 5.29 ± 0.12e | 15.24 ± 0.14d | 14.58 ± 0.20d | 4.15 ± 0.07d | 3.53 ± 0.10d | 26.00 ± 0.18d | 24.42 ± 0.28d |
| 30 | 110 | 4.62 ± 0.09f | 3.48 ± 0.10f | 12.09 ± 0.17e | 11.46 ± 0.16e | 3.00 ± 0.08e | 2.42 ± 0.06e | 18.00 ± 0.24e | 18.57 ± 0.20e |
| 35 | 100 | – | – | – | – | – | – | – | – |

Means are in days with SE and *n* the initial number of eggs observed for each temperature.
Means in each column followed by the same letter are not significantly different (Tukey's HSD, $P = 0.05$).

**Table 2.** Parameters ($a$ = $y$-intercept, $b$ = common slope) and goodness of fit estimators ($R^2$ and AIC) of models fitted to cumulated frequency distributions of development times of *H. hampei* immature stages reared at six constant temperatures.

| | *y*-intercept (*a*) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Life stage | 15°C | 18°C | 20°C | 23°C | 25°C | 30°C | Slope (*b*) | $R^2$ | AIC |
| Egg[1] | −13.76±0.30 | −11.78 ± 0.25 | −10.55 ± 0.23 | −8.96 ± 0.20 | −8.26 ± 0.19 | −7.04 ± 0.17 | 4.74 ± 0.10 | 0.94 | 515.75 |
| Larva[2] | – | −24.19 ± 0.37 | −22.17 ± 0.34 | −19.98 ± 0.31 | −17.78 ± 0.28 | −16.18 ± 0.26 | 6.63 ± 0.10 | 0.96 | 710.44 |
| Pupa[2] | – | −10.46 ± 0.23 | −7.74 ± 0.18 | −6.63 ± 0.16 | −5.19 ± 0.132 | −3.64 ± 0.13 | 4.11 ± 0.09 | 0.97 | 339.76 |
| Egg-adult[1] | – | −37.55 ± 0.58 | −34.19 ± 0.53 | −31.48 ± 0.49 | −28.93 ± 0.45 | −26.54 ± 0.41 | 8.91 ± 0.14 | 0.95 | 1030.14 |

[1]CLL distribution: $f(x) = 1 - \exp(-\exp(a_i + b \ln x))$.
[2]Probit distribution: $f(x) = \emptyset(a_i + b \ln x)$.
Models: CLL and probit distributions: $f(x)$ is the probability to complete development at time $x$, $\ln x$ is the natural logarithm of the days observed, $a_i$ is the intercept of the regression line corresponding to temperature $i$, and $b$ is the common slope of the regression line in all cases.

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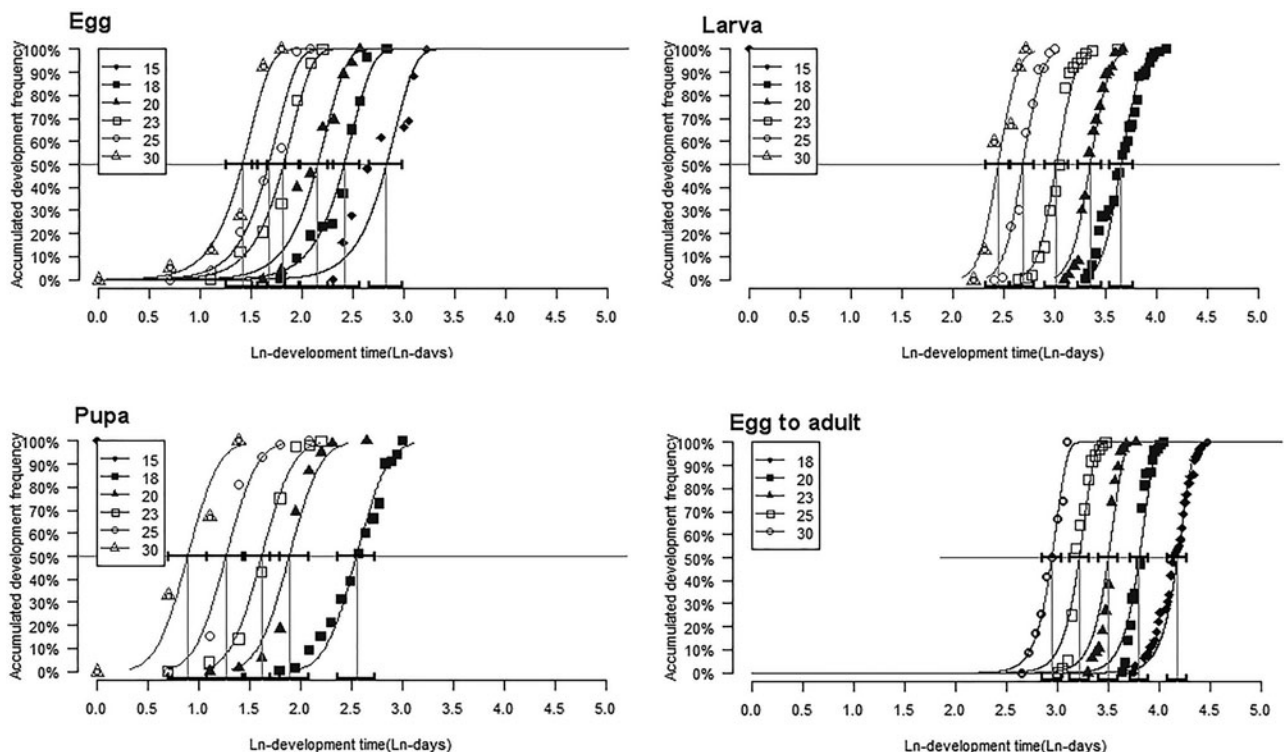


**Fig. 1.** Cumulative distribution of developmental times of *H. hampei* egg, larva, pupa and egg to adult. Curves are fitted models: complementary log–log (CLL) model for egg stage and complete development from egg to adult, and probit model for the larva and pupa stages. Bars indicate 95% confidence intervals for median development times estimated from the models.

**Table 3.** Estimates of the linear regression describing the effect of temperature on *H. hampei* development rate (1/day).

| Life stage | Linear regression equation | *F* | *df* | *P* | $R^2$ | AIC | $T_{min}$(°C) | *k* (DD) |
|---|---|---|---|---|---|---|---|---|
| Egg | $r(T) = -0.1349 + 0.0128 \times T$ | 947.29 | 1, 4 | <0.0001 | 0.99 | 43.08 | 10.54 | 78.13 |
| Larva | $r(T) = -0.0692 + 0.0053 \times T$ | 153.70 | 1, 3 | 0.001 | 0.98 | −37.66 | 13.06 | 188.68 |
| Pupa | $r(T) = -0.4107 + 0.0274 \times T$ | 276.78 | 1, 3 | <0.0001 | 0.98 | −24.13 | 14.99 | 36.49 |
| Egg-adult | $r(T) = -0.0417 + 0.0032 \times T$ | 295.06 | 1, 3 | <0.0001 | 0.99 | −45.89 | 13.03 | 312.5 |

*k*, thermal constant in degree days (DD); $T_{min}$, minimum temperature threshold; $R^2$, coefficient of determination; AIC, Akaike's information criterion.

4.6 ± 0.1 and 16.8 ± 0.5 days at 30 and 15°C, respectively. The longest mean development time for the larva was 39.5 ± 0.6 days at 18°C, while the shortest was 12.5 ± 0.2 days at 30°C. To complete its development to adult, the pupa stage took an average of 13.6 ± 0.3 days at 18°C and 3.0 ± 0.1 days at 30°C. Mean total development time from egg to adult was 63.4 ± 0.8 days at 18°C and, 18.0 ± 0.2 days at 30°C (table 1).

The distribution of development times for egg stage and the complete development from egg to adult was well described by a CLL model ($R^2$ = 0.94–95, AIC = 515.75–1030.1) (fig. 1, table 2). By contrast, the distributions of development times for larva and pupa stages fitted well a probit distribution model (larva: $R^2$ = 0.96, AIC = 710.4; pupa: $R^2$ = 0.97, AIC = 339.8). Simulated values for development time (median development time of the distribution) obtained from these models were consistent with observed development times (mean development times) (table 1), attesting the quality of model fitting.

### Development rate

Temperature had a significant effect on the development rate of immature stages of *H. hampei* as well as on the total development from egg to adult ($P < 0.001$) (tables 3 and 4). Linear models showed that the minimum temperatures required for immature stage development ($T_{min}$) were 10.5, 13.1, 15.0 and 13.0°C, for egg, larva, pupa and egg to adult respectively (fig. 2, table 3). The thermal constants *k* was estimated at 78.1, 188.7, 36.5 and 312.5 DD for egg, larva, pupa and complete development from egg to adult, respectively. The Logan model gave the best fit for the egg and pupa stages ($R^2$ = 0.89–99 and AIC = −45.87 to −2.31) (fig. 2, table 4), while for the larval stage and total development from egg to adult, modified version (five parameters) of the Sharpe and DeMichele model gave the best fit ($R^2$ = 94–0.95 and AIC = −26.09 to −20.3). The maximum temperature threshold ($T_{max}$) was estimated at 35.2, 34.4, 33.9 and 32°C for egg, larva, pupa and from egg to adult, respectively (fig. 2, table 4).

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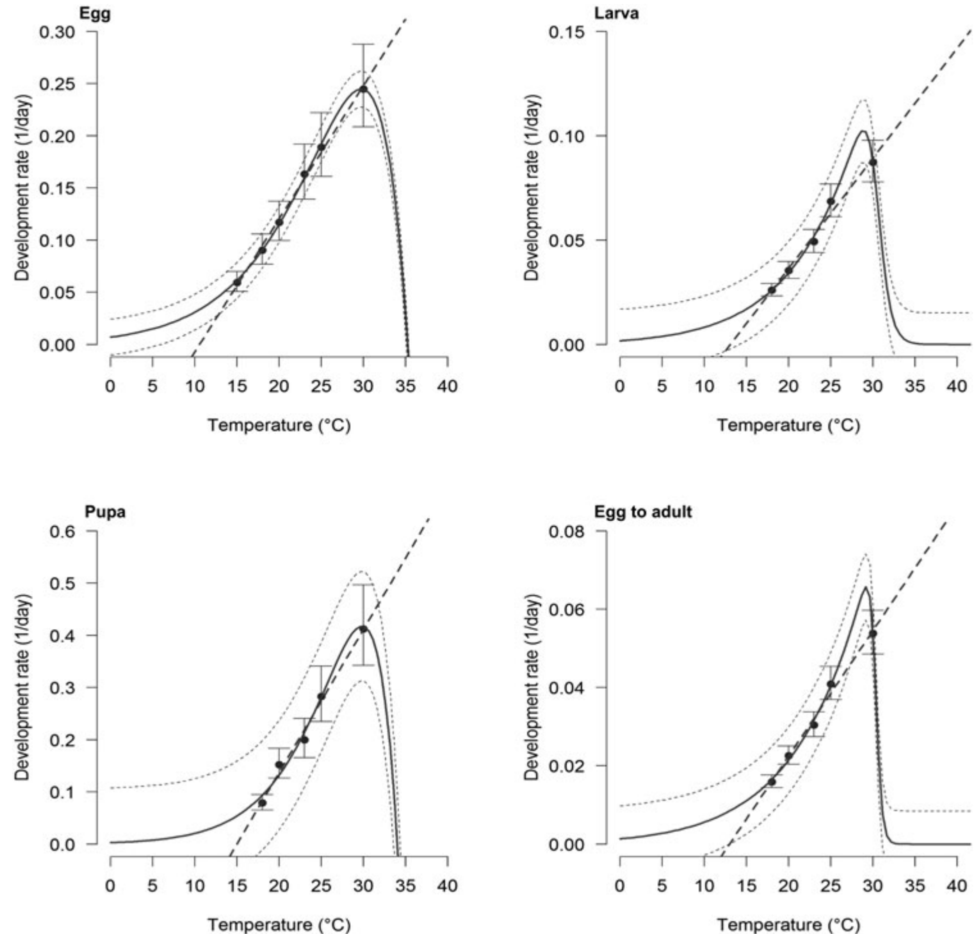


**Fig. 2.** Temperature-dependent developmental rate of *H. hampei* egg, larva, pupa and egg to adult. Observed values are the black points, with bars representing standard deviation of the mean. Fitted models are the dashed straight lines for linear regression and solid lines for the Logan model (egg and pupa) and Sharpe and DeMichele model (larva and egg to adult). Dashed lines above and below represent the upper and lower confidence bands.

### *Effect of temperature on the mortality rate*

Temperature had a significant effect on the mortality rate of the egg and larval stages and for the total development from egg to adult (egg: $F = 68.04$, $df = 2, 3$, $P < 0.05$; larva: $F = 141.45$, $df = 2, 3$, $P < 0.01$; egg to adult: $F = 59.76$, $df = 2, 4$, $P < 0.05$) (table 5). However, the tested temperatures did not have a significant effect on the mortality of the pupa stage ($F = 14.73$, $df = 1, 3$, $P = 0.18$). For all immature stages, the best-fitted model was the Wang 2 ($R^2 = 0.98$–$0.99$ and AIC between −22.92 and −21.20), while second-order polynomial functions gave a good fit to mortality for the total development from egg to adult ($R^2 = 0.98$, AIC = −14.9) (fig. 3, table 5). The larval stage had the highest mortality rate for the tested temperatures with 100, 50, 38, 28, 33 and 80% at 15, 18, 20, 23, 25 and 30°C, respectively (fig. 3). The thermal window for *H. hampei* survival from egg to adult was estimated from the second order polynomial function between 16.1 and 30.3°C, and the optimum temperature for survival was estimated at 23.2°C (fig. 3).

## Discussion

### *Observation method*

Here, we developed and validated a new observation method that allowed direct monitoring of the complete development from egg to adult of a large number of *H. hampei* individuals, whilst maintaining rearing conditions similar to those found in a coffee berry. This is the recommended approach for accurate assessment of the impact of temperature on insect demography (Tonnang *et al*., 2013). Due to the cryptic nature of the pest, life cycle observation has been challenging in the past. Different methods and approaches were used in both field and laboratory that include those in Baker *et al*. (1992), where coffee berries on trees in the field were artificially infested with *H. hampei* and sampled after every 3–4 days for dissection to observe immature stages. Fernández & Cordero (2007) used parchment coffee beans moistened for 24 h to feed the larval stage in the laboratory. By contrast, Brun *et al*. (1993) reared *H. hampei* on artificial diets in the laboratory, which made the observation easier. However, artificial diets are but proxies to natural food for *H. hampei* and thus might affect the development process of the pest. In the recent past, Jaramillo *et al*. (2009) developed an observation technique based on artificial infestation of coffee berries in the laboratory, where berries were dissected on a daily basis to observe the development of groups of individuals. The most innovative improvement of our method is probably the way we monitored the larva development on fresh coffee seeds and followed the same individuals from egg through to the adult stage. On the one hand, packing the fresh coffee seed hosting the larva in an aluminium foil allowed us to mimic the living conditions inside the berry, especially darkness and high level of humidity. On

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**Table 4.** Model parameters of Logan and Sharpe and DeMichele models describing the effect of temperature on *H. hampei* immature stage development rate (1/day).

| Life stage | Model | Parameters | | $F$ | $df$ | $P$ | $R^2$ | AIC |
|---|---|---|---|---|---|---|---|---|
| Egg | Logan | $Y$ | 0.018 ± 0.001 | 490.91 | 2, 3 | 0.002 | 0.99 | −45.87 |
| | $r(T) = Y\left\{\exp(\rho T) - \exp\left(\rho\, T_{max} - \frac{(T_{max} - T)}{v}\right)\right\}$ | $T_{max}$ | 35.232 ± 0.001 | | | | | |
| | | $\rho$ | 0.175 ± 1.097 | | | | | |
| | | $v$ | 5.288 ± 0.010 | | | | | |
| Larva | Sharpe and DeMichele | $P$ | 0.179 ± 0.059 | 40.62 | 2, 3 | <0.001 | 0.94 | −20.30 |
| | $r(T) = \frac{P \cdot T/T_o \cdot \exp[\Delta H_A/R(1/T_o - 1/T)]}{1 + \exp[\Delta H_L/R\ (1/T_L - 1/T)]}$ | $T_o$ | 303.459 ± 0.057 | | | | | |
| | | $H_A$ | − 232,290.3 ± 0.000 | | | | | |
| | | $T_L$ | 303.657 ± 0.168 | | | | | |
| | | $H_L$ | − 255,315.2 ± 0.000 | | | | | |
| Pupa | Logan | $Y$ | 0.004 ± 0.003 | 29.37 | 1, 3 | <0.001 | 0.89 | −2.31 |
| | $r(T) = Y\left\{\exp(\rho T) - \exp\left(\rho\, T_{max} - \frac{(T_{max} - T)}{v}\right)\right\}$ | $T_{max}$ | 33.993 ± 0.041 | | | | | |
| | | $\rho$ | 0.227 ± 7.865 | | | | | |
| | | $v$ | 3.920 ± 0.084 | | | | | |
| Egg-adult | Sharpe and DeMichele | $P$ | 0.013 ± 0.001 | 47.31 | 1, 3 | <0.001 | 0.95 | −26.09 |
| | $r(T) = \frac{P \cdot T/T_o \cdot \exp[\Delta H_A/R(1/T_o - 1/T)]}{1 + \exp[\Delta H_L/R\ (1/T_L - 1/T)]}$ | $T_o$ | 289.44 ± 0.000 | | | | | |
| | | $H_A$ | 21,589.23 ± 0.000 | | | | | |
| | | $T_L$ | 303.48 ± 0.069 | | | | | |
| | | $H_L$ | 517,475.3 ± 0.000 | | | | | |

For Logan models $Y$, $\rho$ and $v$, model parameters (mean ± SE); $T_{max}$, maximum temperature threshold (in °C); and for Sharpe and DeMichele model, $P$, $T_o$, $H_A$, $T_L$ and $H_L$, model parameters (mean ± SE); $R$ is the universal gas constant (1.987 cal degree$^{-1}$ mol$^{-1}$), $F$, $F$-test statistic; $df$, degree of freedom; $P$, probability value; $R^2$, coefficient of determination; AIC, Akaike's information criterion.

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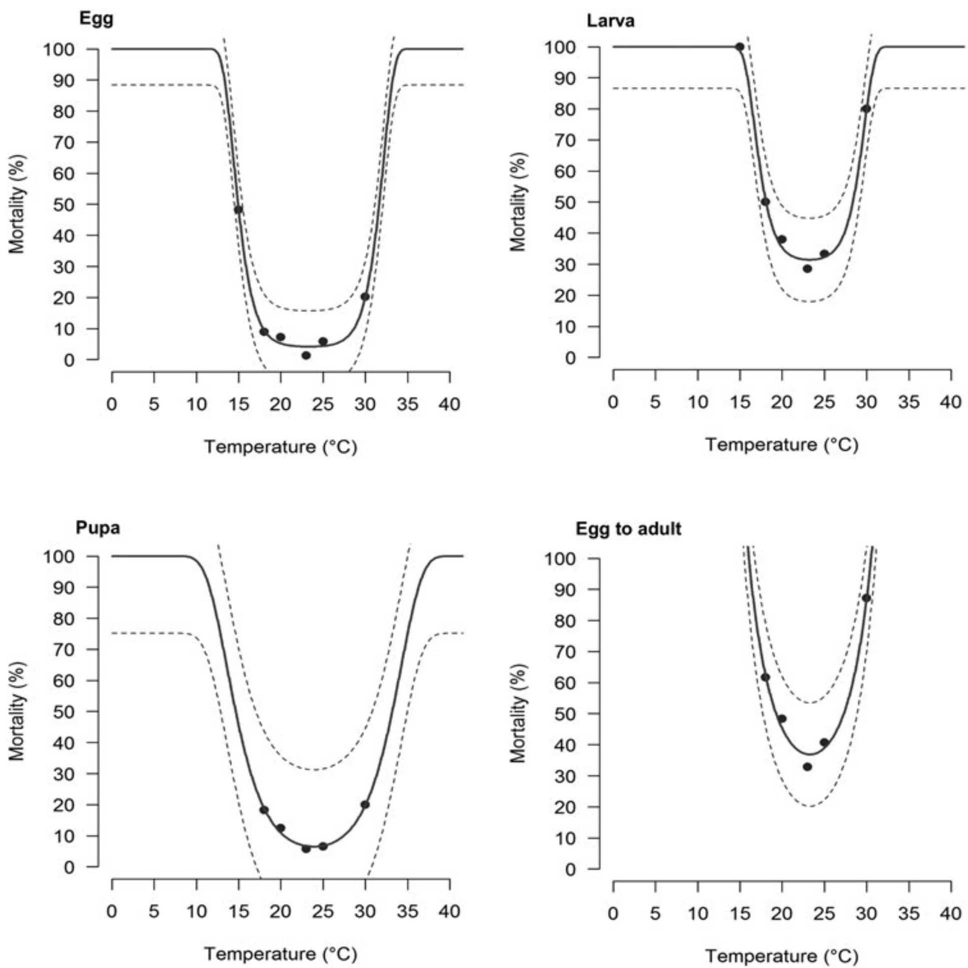


**Fig. 3.** Temperature-dependent mortality rate of *H. hampei* immature stages fitted to Wang 2 function for egg, larva and pupa, and to second order polynomial function for the complete development from egg to adult. The points are observed values and the solid curves are the selected model output. Dashed lines above and below represent the upper and lower 95% confidence bands of the models.

the other hand, the aluminium package was easily opened without damaging or disturbing the larva, which is not ensured when berries are dissected. This method will be adapted to assess *H. hampei* female fecundity and adult longevity for the calculation of life table parameters.

### Temperature-dependent development models

Although insects do not develop at a constant temperature in nature, development models obtained from laboratory studies provide useful information on their thermal biology, such as thermal thresholds. As such, they help understand and predict the pest distribution and population dynamics in plantations according to temperature (Tonnang *et al*., 2013; Azrag *et al*., 2018). To the best of our knowledge, the only study that adopted a similar approach for *H. hampei* is that of Jaramillo *et al.* (2009). In that study, a combination of a linear regression and the modified version of the Logan model was used to characterize the relationship between the development rate and temperature for all life stages. In our study, ILCYM software was used to fit the linear regression and to select the best nonlinear model amongst 58 models used to describe this relationship for insects (Tonnang *et al*., 2013).

The linear model well predicted the development rate for all the tested temperatures, confirming what has been found for a number of insect species, including *H. hampei* (Sporleder *et al*., 2004; Jaramillo *et al*., 2009; Azrag *et al*., 2017). The Logan and five parameters of the Sharpe and DeMichele models (Logan *et al*., 1976; Sharpe & DeMichele, 1977) were the best nonlinear models. The biophysical model of Sharpe & DeMichele has a biological significance in predicting insect development rate (Sharpe & DeMichele, 1977). It includes thermodynamic parameters associated with the development, such as the enthalpy of enzyme activation (Sharpe & DeMichele, 1977). In addition, the model can be fitted in different forms (i.e. four, five and six parameters), which makes it flexible in fitting different temperature ranges (Tonnang *et al*., 2013). On the other hand, Logan model (Logan *et al*., 1976) has a restricted number of parameters and it considers enzyme-catalysed biochemical reaction rate at optimum temperature.

For the mortality rate, the best model was the Wang 2 model (Wang *et al*., 1982). This model gives a very good fit to the data over a wide range of constant temperatures (Tonnang *et al*., 2013). It showed that the mortality rate of *H. hampei* immature stages was around 100% at 13°C but, decreased with an increase in temperature and reached a minimum value at 23°C. Thereafter, the mortality increased again and reached 100% at around 34°C for

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**Table 5.** Model parameters of Wang 2 function (Tl, *h*, *B* and *H* ± SE) and second order polynomial function ($b_1$, $b_2$ and $b_3$ ± SE) testing temperature effect on *H. hampei* immature stage mortality rate.

| Life stage | Model | Parameters | | *F* | *df* | *P* | $R^2$ | AIC |
|---|---|---|---|---|---|---|---|---|
| Egg | | Tl | 18.516 ± 1.548 | 68.04 | 2, 3 | 0.015 | 0.99 | −22.92 |
| | | Th | 28.031 ± 1.278 | | | | | |
| | | *B* | 1.289 ± 0.358 | | | | | |
| | | *H* | 0.040 ± 0.021 | | | | | |
| Larva | Wang 2 | Tl | 28.492 ± 0.000 | 141.45 | 2, 3 | 0.007 | 0.99 | −21.20 |
| | $m\ (T) = 1 - \frac{1}{\exp\left((1 + \exp(-T - \mathrm{Tl}/\ B)) \times (1 + \exp(-\ \mathrm{Th} - T/B)) \times H\right)}$ | Th | 17.933 ± 0.000 | | | | | |
| | | *B* | 1.234 ± 0.000 | | | | | |
| | | *H* | $1 \times 10^{-04}$ ± 0.000 | | | | | |
| Pupa | | Tl | 23.911 ± 0.233 | 14.73 | 1, 3 | 0.188 | 0.98 | −23.23 |
| | | Th | 23.912 ± 0.233 | | | | | |
| | | *B* | 2.521 ± 0.281 | | | | | |
| | | *H* | 0.017 ± 0.003 | | | | | |
| Egg-adult | Second order polynomial function | $b_1$ | 9.329 ± 0.001 | 59.76 | 2, 4 | 0.016 | 0.98 | −14.91 |
| | $m\ (T) = \exp\ (b_1 + b_2T + b_3T^2)$ | $b_2$ | −0.887 ± 0.007 | | | | | |
| | | $b_3$ | 0.0191 ± 0.000 | | | | | |

*F*, *F*-test statistic; *df*, degree of freedom; *P*, probability value; $R^2$, coefficient of determination; AIC, Akaike's information criterion.

all immature stages. This model was previously used to predict the relationship between temperature and mortality of immature stages for different tropical pests, such as the mealybug *Phenacoccus solenopsis* Tinsley (Fand *et al*., 2014) and the leaf miner *Liriomyza huidobrensis* Blanchard (Mujica *et al*., 2017).

### Life cycle

The complete life cycle of *H. hampei* was obtained under constant temperature in the range 18–30°C, with a total developmental time of about 63 days at 18°C and 18 days at 30°C. The egg incubation period ranged from 4.6–16.9 days under a temperature range of 30–15°C, and it might have been slightly underestimated with our method (by a day less). Jaramillo *et al*. (2009) reported an egg incubation period of 4.7–12.0 days under the temperature range 33–20°C. In that study, the authors did not get oviposition by females at 15°C. Our result at 25°C is similar to that reported by Brun *et al*. (1993), who obtained an incubation period of 5 days at the same temperature for a population reared on an artificial diet. On the other hand, Ruiz *et al*. (1996) found an incubation period (3.3 days) at 26°C shorter than ours. The variation in incubation period between these studies may be linked to the methods used to produce eggs for the experiments and to the incubation conditions, such as observation settings, relative humidity and photoperiod, which might have played a role.

For larval stage, development times we obtained are in agreement with findings of Jaramillo *et al*. (2009) for all tested temperatures, with the exception of those obtained at 23°C. These authors reported a larval development time of 17 days, which differs from 21 days we reported here. In fact, in our study, only 12 individuals completed the larval stage in 17 days, which is the lowest value at 23°C. By contrast, 80% of the individuals completed this stage in a time between 20 and 23 days. The larva development time assessed by Chami (2003) at 25°C (28.1 days) was much longer than ours (15.2 days) at the same temperature. Here again, these variations may be due to methods and conditions used to maintain and monitor *H. hampei* larvae. The development time of pupa we obtained at 25°C was similar to those recorded by Bergamin (1943) and Chami (2003).

### Thermal requirements

The minimum temperature thresholds ($T_{min}$) we obtained are similar to those reported by Jaramillo *et al*. (2009), with the exception of the egg stage, for which we found 10.5°C compared to 16.7°C in that study. The thermal constant for the complete development from egg to adult in our study (312.5 DD) is also comparable to the 262.5 DD reported in the study by Jaramillo *et al*. (2009). Again, differences may be due to experimental conditions and observation methods. Another explanation may be that *H. hampei* individuals used in Jaramillo *et al*. (2009) were collected in a different region in Kenya, with a different climate. We cannot rule out that populations from different geographical areas have slightly different thermal requirements.

Our models gave a thermal window of 13–32°C for *H. hampei* to complete its development from egg to adult. On the other hand, the thermal window for survival obtained from mortality models is narrower with about 16–30°C, with optimal temperature for survival around 23°C. This is in line with other studies that showed that insect development rate response to temperature is different from survival response, due to some other factors such as the diet and manipulations, which contribute to the mortality rate beside temperature (Sporleder *et al*., 2004; Mujica *et al*., 2017). For example, this was true for the survival response to temperature of the whitefly *Bemisia tabaci* (Gennadius) and the leaf miner *L. huidobrensis* (Blanchard), which differed from developmental rate response (Bonato *et al*., 2007; Mujica *et al*., 2017).

### Implication for pest management

Arabica coffee does not tolerate too high temperature and the crop is usually grown high in tropical mountains or highlands. The range of elevation favouring Arabica coffee cultivation varies considerably across the tropical belt; in east Africa, the crop is usually found in the range 1000–2000 m asl (Garedew *et al*., 2017; Liebig *et al*., 2018). There, *H. hampei* usually thrives in coffee plantations below 1400 m asl, where the climate is warmer. At world scale, most studies showed that infestation by the pest decreases with an increase in elevation (e.g. Jaramillo *et al*., 2011; Avelino *et al*., 2012). According to our results, the temperature range 20–28°C is the most suitable for *H. hampei* immature stage development and a constant temperature of 23°C is optimal for their survival. Such temperature range roughly matches conditions of low elevation plantations of Arabica coffee in east Africa, where *H. hampei* causes the highest damage to the crop (Jaramillo *et al*., 2011). Our results therefore confirm that, provided that *H. hampei* fecundity relationship to temperature shows a similar trend, low-elevation coffee in east Africa should be considered as the highest in terms of infestation risk by the coffee berry borer and should focus attention on its management.

Another major factor impacting temperature in coffee plantations is shade. As an understorey plant, coffee grows well under shading trees and shading canopy largely affects pests and diseases through microclimate. For *H. hampei*, a well-managed shade is sometimes considered as a promising strategy to reduce the temperature and keep pest outbreaks at bay (e.g. Teodoro *et al*., 2009; Jaramillo *et al*., 2011). However, the impact of shade on coffee infestation by *H. hampei* is far from obvious and mechanisms involved are complex (Avelino *et al*., 2012; Jonsson *et al*., 2015; Mariño *et al*., 2016). Our results will help understand the impact of shade on *H. hampei* populations through microclimate and thus will contribute to more precise and efficient recommendations for shade management on coffee.

Finally, climate change is expected to impact the distribution of many insect pests worldwide. For *H. hampei*, the threat is expected to worsen in east Africa, with the extension of the distribution to coffee areas at altitudes higher than today, where Arabica coffee is particularly renowned for its quality (Jaramillo *et al*., 2011). The models we developed in the present study will help predict *H. hampei* distribution under global warming and assess the risk in terms of production loss. Our study will therefore contribute to improving mitigation strategies against this important pest.

## Conclusions

In conclusion, we developed an observation method that allowed for the first time the monitoring of the development of the same individuals of *H. hampei* from egg to adult. The models presented here gave good predictions for immature stage development and survival according to temperature. Models also provided thermal requirements for immature stage development. With the incorporation of oviposition models and validation under fluctuating temperature, it will help understand and

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predict *H. hampei* distribution on coffee production areas. This information will be incorporated in pest management programmes for better control of this major pest of coffee, in the context of climate change.

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## References

**Avelino J, Romero-Gurdián A, Cruz-Cuellar HF and Declerck FAJ** (2012) Landscape context and scale differentially impact coffee leaf rust, coffee berry borer, and coffee root-knot nematodes. *Ecological Applications* **22**, 584–596.

**Azrag AGA, Murungi LK, Tonnang HE, Mwenda D and Babin R** (2017) Temperature-dependent models of development and survival of an insect pest of African tropical highlands, the coffee antestia bug *Antestiopsis thunbergii* (Hemiptera: Pentatomidae). *Journal of Thermal Biology* **70**, 27–36.

**Azrag AGA, Pirk CWW, Yusuf AA, Pinard F, Niassy S, Mosomtai G and Babin R** (2018) Prediction of insect pest distribution as influenced by elevation: combining field observations and temperature-dependent development models for the coffee stink bug, *Antestiopsis thunbergii* (Gmelin). *PLoS One* **13**, e0199569.

**Baker PS, Barrera JF and Rivas A** (1992) Life history studies on the coffee berry borer (*Hypothenemus hampei*, Scolytidae) on coffee trees in southern Mexico. *Journal of Applied Ecology* **29**, 656–662.

**Barrera JF** (1994) *Dynamique des populations du scolyte des fruits du caféier,* Hypothenemus hampei *(Coleoptera: Scolytidae), et lutte biologique avec le parasitoide Cephalonomia stephanoderis (Hymenoptera: Bethylidae), au Chiapas, Mexique*. PhD Thesis, Université Paul-Sabatier, Toulouse III, France, 301 p.

**Bergamin J** (1943) Contribuição para o conhecimiento da biología da broca do café *Hypothenemus hampei* (Ferrari, 1867) (Col: Ipidae). *Archives of the Institute of Biology* **14**, 31–72.

**Bonato O, Lurette A, Vidal C and Fargues J** (2007) Modelling temperature-dependent bionomics of *Bemisia tabaci* (Q-biotype). *Physiological Entomology* **32**, 50–55.

**Brun LO, Marcillaud C, Gaudichon V and Suckling DM** (1989) Endosulfan resistance of *Hypothenemus hampei* (Coleoptera: Scolytidae) in New Caledonia. *Journal of Economic Entomology* **82**, 1311–1316.

**Brun LO, Gaudichon V and Wigley PJ** (1993) An artificial diet for continuous rearing of the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Scolytidae). *International Journal of Tropical Insect Science* **14**, 585–587.

**Chami A** (2003) *Biología de la broca del café* Hypothenemus hampei *Ferrari 1867.(Coleoptera: Scolytidae)*. Tesis, Decanato de Agronomía, Universidad Centroccidental Lisandro Alvarado, 29 p.

**Damon A** (2000) A review of the biology and control of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Bulletin of Entomological Research* **90**, 453–465.

**Dufour BP and Frérot B** (2008) Optimization of coffee berry borer, *Hypothenemus hampei* Ferrari (Col., Scolytidae), mass trapping with an attractant mixture. *Journal of Applied Entomology* **132**, 591–600.

**Fand BB, Tonnang HE, Kumar M, Kamble AL and Bal SK** (2014) A temperature-based phenology model for predicting development, survival and population growth potential of the mealybug, *Phenacoccus solenopsis* Tinsley (Hemiptera: Pseudococcidae). *Crop Protection* **55**, 98–108.

**Fernández S and Cordero J** (2007) Biología de la broca del café *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae: Scolytinae) en condiciones de laboratorio. *Bioagro* **19**, 35–40.

**Garedew W, Lemessa F and Pinard F** (2017) Assessment of berry drop due to coffee berry disease and non-CBD factors in Arabica coffee under farmers fields of southwestern Ethiopia. *Crop Protection* **98**, 276–282.

**Jaramillo J, Borgemeister C and Baker P** (2006) Coffee berry borer *Hypothenemus hampei* (Coleoptera: Curculionidae): searching for sustainable control strategies. *Bulletin of Entomological Research* **96**, 223–233.

**Jaramillo J, Chabi-Olaye A, Kamonjo C, Jaramillo A, Vega FE, Poehling HM and Borgemeister C** (2009) Thermal tolerance of the coffee berry borer *Hypothenemus hampei*: predictions of climate change impact on a tropical insect pest. *PLoS One* **4**, e6487.

**Jaramillo J, Chabi-Olaye A and Borgemeister C** (2010) Temperature-dependent development and emergence pattern of *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae) from coffee berries. *Journal of Economic Entomology* **103**, 1159–1165.

**Jaramillo J, Muchugu E, Vega FE, Davis A, Borgemeister C and Chabi-Olaye A** (2011) Some like it hot: the influence and implications of climate change on coffee berry borer (*Hypothenemus hampei*) and coffee production in East Africa. *PLoS One* **6**, e24528.

**Jonsson M, Raphael IA, Ekbom B, Kyamanywa S and Karungi J** (2015) Contrasting effects of shade level and altitude on two important coffee pests. *Journal of Pest Science* **88**, 281–287.

**Le Pelley RH** (1968) *Pests of Coffee*. London: Longmans Green and Co, 590 p.

**Liebig T, Babin R, Ribeyre F, Läderach P, van Asten P, Poehling H-M, Jassogne L, Cilas C and Avelino J** (2018) Local and regional drivers of the African coffee white stem borer (*Monochamus leuconotus*) in Uganda. *Agricultural and Forest Entomology* **20**, 514–522.

**Logan JA, Wollkind DJ, Hoyt SC and Tanigoshi LK** (1976) An analytic model for description of temperature dependent rate phenomena in arthropods. *Environmental Entomology* **5**, 1133–1140.

**Mariño YA, Pérez ME, Gallardo F, Trifilio M, Cruz M and Bayman P** (2016) Sun vs. shade affects infestation, total population and sex ratio of the coffee berry borer (*Hypothenemus hampei*) in Puerto Rico. *Agriculture, Ecosystems & Environment* **222**, 258–266.

**Mujica N, Sporleder M, Carhuapoma P and Kroschel J** (2017) A temperature-dependent phenology model for *Liriomyza huidobrensis* (Diptera: Agromyzidae). *Journal of Economic Entomology* **110**, 1333–1344.

**Nielsen AL, Hamilton GC and Matadha D** (2008) Developmental rate estimation and life table analysis for *Halyomorpha halys* (Hemiptera: Pentatomidae). *Environmental Entomology* **37**, 348–355.

**O'Hara RB and Kotze DJ** (2010) Do not log-transform count data. *Methods in Ecology and Evolution* **1**, 118–122.

**Ovuka M and Lindqvist S** (2000) Rainfall variability in Murang'a District, Kenya: meteorological data and farmers' perception. *Physical Geography* **82**, 107–119.

**Pardey AEB** (2015) Coffee insect pests part II: damage caused by arthropods. In Gaitán AL (ed), *Compendium of Coffee Diseases and Pests*. St Paul, USA: APS Press, The American Phytopathological Society, pp. 1–62.

**R Development Core Team**. (2016) *R: a Language and Environment for Statistical Computing*. Austria, R Foundation for Statistical Computing. Available online at https://www.R-project.org/.

**Régnière J, Powell J, Bentz B and Nealis V** (2012) Effects of temperature on development, survival and reproduction of insects: experimental design, data analysis and modeling. *Journal of Insect Physiology* **58**, 634–647.

**Ruiz L, Bustillo-Panley AE, Flórez FJP and González MT** (1996) Ciclode vida de *Hypothenemus hampei* en dos dikfas melúdicas. *Cenicafé* **47**, 77–84.

**Sharpe PJ and DeMichele DW** (1977) Reaction kinetics of poikilotherm development. *Journal of Theoretical Biology* **64**, 649–670.

**Sporleder M, Kroschel J, Quispe MRG and Lagnaoui A** (2004) A temperature-based simulation model for the potato tuberworm, *Phthorimaea operculella* Zeller (Lepidoptera; Gelechiidae). *Environmental Entomology* **33**, 477–486.

**Teodoro AV, Tscharntke T and Klein AM** (2009) From the laboratory to the field: contrasting effects of multi-trophic interactions and agroforestry management on coffee pest densities. *Entomologia Experimentalis et Applicata* **131**, 121–129.

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**Tonnang EZH, Juarez H, Carhuapoma P, Gonzales JC, Mendoza D, Sporleder M, Simon R and Kroschel J** (2013) ILCYM – Insect Life Cycle Modeling. A software package for developing temperature-based insect phenology models with applications for local, regional and global analysis of insect population and mapping. Lima, Peru, International Potato Center, 193 p.

**Vega FE, Blackburn MB, Kurtzman CP and Dowd PF** (2003) Identification of a coffee berry borer associated yeast: does it break down caffeine? *Entomologia Experimentalis et Applicata* **107**, 19–24.

**Vega FE, Infante F, Castillo A and Jaramillo J** (2009) The coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera: Curculionidae): a short review, with recent findings and future research directions. *Terrestrial Arthropod Reviews* **2**, 129–147.

**Wagner TL, Wu HI, Sharpe PJH and Coulson RN** (1984) Modelling distributions of insect development time: a literature review and application of the Weibull function. *Annals of the Entomological Society of America* **77**, 475–487.

**Wagner TL, Olson RL and Willers JL** (1991) Modeling arthropod development time. *Journal of Agricultural Entomology* **8**, 251–270.

**Wang RS, Lan ZX and Ting YC** (1982) Studies on mathematical models of the relationships between insect development and temperature. *Acta Ecologica Sinica* **2**, 47–57.

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