Modelling the effect of temperature on the biology and demographic parameters of the African coffee white stem borer, *Monochamus leuconotus* (Pascoe) (Coleoptera: Cerambycidae)

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Highlights

• Temperature-dependent development models were developed for *Monochamus leuconotus*.

• T_{min} for immature stage development ranged from 10 to 11.5 °C, depending on the stage.

• T_{max} for the development was estimated between 37.4 and 40.6 °C, depending on the stage.

• The fecundity was highest at 23 °C, with 97.8 eggs per female.

• Intrinsic rate of increase r_m was maximal between 26 and 28 °C, with a value of 0.008

Abstract

The African coffee white stem borer *Monochamus leuconotus* (Pascoe) (Coleoptera: Cerambycidae) is a destructive insect pest of Arabica coffee trees in African highlands. Our study aims to provide information on the pest biology as influenced by temperature, determine thermal thresholds, and provide life table parameters for *M. leuconotus* reared in the laboratory. The life cycle of *M. leuconotus* was studied at seven constant temperatures in the range 15-35°C, with 80 ± 5% RH and a photoperiod of L:D 12:12. Linear and nonlinear models were fitted to laboratory data to describe the impact of temperature on *M. leuconotus* development, mortality, fecundity and senescence. The complete life cycle was obtained between 18 and 30°C, with the egg incubation period ranging 10.8-29.2 days. The development time was longest for the larva, with 194.2 days at 30°C and 543.1 days at 18°C. The minimum temperature threshold (T_{min}) was estimated at 10.7, 10.0 and 11.5°C, for egg, larva and pupa, respectively. The maximum temperature threshold (T_{max}) was estimated at 37.4, 40.6 and 40.0°C for egg, larva and pupa, respectively. The optimum temperature for immature stage survival was estimated between 23.0 and 23.9°C. The highest fecundity was 97.8 eggs per female at 23°C. Simulated life table parameters showed the highest net reproductive rate (R_o) of 11.8 daughters per female at 26°C and maximal intrinsic rate of increase (r_m) between 26 and 28°C, with a value of 0.008. Our results will help understanding *M. leuconotus* biology as influenced by temperature and may be used to predict the distribution and infestation risk under climate warming for this critical coffee pest.

Keywords: *Coffea arabica*, insect life cycle modelling, development time, development rate, life table parameters.

1. Introduction

During the last 20 years, the consequences of global warming on the distribution and phenology of species (Parmesan & Yohe, 2003) or on community diversity and ecosystem functioning (Lavergne *et al*., 2010) have been widely explored. Temperature has been shown to be a key factor for fitness or performance-related traits of ectothermic species (Kingsolver *et al*., 2009; Estay *et al*., 2011; Paaijmans *et al*., 2013). Insect populations are expected to increase more rapidly in a warmer world (Morris *et al*., 2008). Thus, determining thermal requirements and so optimal values for species development appears of major interest to understand species repartition.

The long-horned beetles under genus *Monochamus* contain approximately 150 species, most of them being important pests in agriculture and forestry, as well as vectors of diseases (Naves *et al*., 2008). *Monochamus leuconotus* (Pascoe, 1869) (Coleoptera: Cerambycidae) is one of the most economically threatening insect pests of Arabica coffee in Africa (Gichuhi *et al*., 2017; Liebig *et al*., 2018), with a distribution in Western, Eastern, Central and Southern parts of the continent (Schoeman *et al*., 1998; Rutherford & Phiri, 2006; Egonyu *et al*., 2015). It was first reported in the 1860s in South Africa, and then in the 1930s in Eastern Africa (Kenya), attacking Arabica coffee at elevations below 1600 m asl (Knight, 1939; Tapley, 1960; Schoeman *et al.*, 1998). Currently, *M. leuconotus* is ranked as the most or the second most important pest of Arabica coffee after the coffee berry borer *Hypothenemus hampei* (Ferrari) in several countries including Tanzania, Uganda, Malawi and Zimbabwe, where infestation rates in farms were reported to be between 70 and 90% (Erbaugh *et al*., 2008; ICC, 2008; Egonyu *et al*., 2015). It is therefore of great importance to investigate the effect of temperature on the life history traits of this insect in order to better predict its actual repartition and potential expansion.

Eggs of *M. leuconotus* are inserted by the reproductive females in the bark of coffee stems or main branches. The young larvae feed on the bark of the coffee trees damaging phloem, whereas older larvae bore galleries into the wood. Wood tunnelling and ring barking weaken the trees and disrupt sap flow leading to significant damage including yellowing of the leaves, stunted growth, and dieback (Jonsson *et al*., 2015). While feeding, adults cause lesions to the buds, shoots, stem bark and skin of the green berries. Younger trees are more susceptible to *M. leuconotus* infestation and trees less than three year old are often killed (Jonsson *et al*., 2015). Older trees can survive but become less productive. In Africa, production loss due to *M. leuconotus* is estimated at 25% (Rutherford & Phiri, 2006). In the past, organochlorine insecticides were used to control the pest, but nowadays they are totally banned and there is no chemical alternative as effective (ICC, 2008; Jayaraj *et al*., 2016). More traditional control methods are used by farmers as alternatives to chemical control. They include cutting and burning the infested stems, driving a wire into the galleries to kill the larvae and pupae, picking the adults and covering the coffee tree stem with banana leaves to prevent females from laying eggs (McNutt, 1975; Rutherford & Phiri, 2006). These methods are not effective enough to keep crop loss below economic injury level and, nowadays, some coffee production areas in east Africa are experiencing an alarming resurgence of the pest (Jonsson *et al*., 2015).

Despite the significant impact of *M. leuconotus* on coffee production, little is known about its biology and ecology. The pest spends the major part of its life (up to 2 years) inside the coffee wood, which makes it difficult to observe its development. Tapley (1960) reported a complete life cycle of 24 months under field conditions. Similarly, Schoeman *et al*. (1998) recorded a duration of 18 to 24 months in infested coffee logs kept in the laboratory. A recent study by Gichuhi *et al*. (2017) reported a complete life cycle of about 14 months at 25°C, with a mean fecundity of 40

eggs per female, when reared on an artificial diet in the laboratory. The relationship between *M. leuconotus* life cycle and temperature has not been elucidated so far. The knowledge of the pest thermal requirements however is a crucial prerequisite for predicting the pest population dynamics and implementing well-prepared and more targeted management strategies (Régnière *et al*., 2012).

In insects, the responses of survival, development and reproduction to temperature can be modelled using mathematical functions (Tonnang *et al*., 2013; Dhillon & Hasan, 2017; Pachú *et al*., 2018). Linear model for example is widely used to describe the relationship between development rate and temperature (e.g. Nielsen *et al*., 2008). Combined with non-linear models for extreme temperatures, it allows the calculation of standards parameters such as temperature thresholds for development and the thermal constant (Briere *et al*., 1999; Kontodimas *et al*., 2004). Thus, the present study aims to provide the thermal requirements for *M. leuconotus* population reared under controlled conditions using linear and nonlinear models. In the second step, the models were compiled and used to simulate the life table parameters under different temperatures.

2. Materials and Methods

2.1. Colony initiation and egg production

Insects used for this study were obtained from a colony maintained by Gichuhi *et al*. (2017) in the coffee laboratory of the International Centre of Insect Physiology and Ecology (*icipe*), Nairobi, Kenya. The authors initiated the *M. leuconotus* colony with larvae and pupae extracted from infested coffee stems obtained from coffee farms located on Mt. Kilimanjaro, Tanzania, and reared at 25°C ± 0.5°C, RH 80 ± 5% using an artificial diet (see Gichuhi *et al*., 2017 for the rearing method). In the present study, eggs were obtained from the mated adults (20 males and 30 females) of the first laboratory generation reared by Gichuhi *et al*. (2017). These adults emerged in two

groups; the first group (A) consisted of 12 males and 16 females, whereas the second group (B) consisted of 8 males and 14 females. Adults of the second group emerged three months after adults of the first group in average. Adults from group A were introduced into 4 Plexiglas cages (50 cm long, 40 cm wide and 80 cm high), within each cage 3 males and 4 females. Adults from group B were introduced in 4 cages, within each cage 2 males and 3 or 4 females. Each cage had 6 freshly cut coffee sticks (50 cm long) as support for adult feeding and egg laying (eggs are inserted in the bark). The coffee sticks were slightly buried in a container with moist soil to avoid drying. Wet cotton bolls were provided in the container as a water source. The sticks were removed every 24 h from the Plexiglas cages to extract the eggs and thereafter replaced with new ones.

2.2. Immature stages development and survival

Freshly laid eggs of less than 24 h were carefully extracted from the sticks by cutting the bark around the eggs using a sharp scalpel blade, in such a way that eggs were still wrapped in a fine layer of phloem and wood. The extracted parts with eggs were introduced individually into small plastic containers (3.5 cm depth x 3.9 cm diameter) lined with wet cotton wool covered with a fine layer of sand and a paper towel at the top in order to maintain high humidity in the container. The extracted part was placed on the paper towel and containers closed with lids containing windows made of fine muslin cloth (0.1 µm) for ventilation. The containers were randomly distributed and kept for five days in incubators (SANYO MIR-553 and MIR-554, Sanyo Electrical Ltd., Tokyo, Japan) set at the following seven constant temperatures:15, 18, 20, 23, 25, 30 and 35°C (± 0.5°C), with RH between 75 and 85%, and photoperiod 12:12 L:D. After this period, the phloem got dry and it was carefully separated from the wood, in order to facilitate egg observation. The number of eggs used for the experimentation was 50, 76, 100, 85, 81, 92 and 53, at constant temperatures

of 15, 18, 20, 23, 25, 30 and 35°C (± 0.5°C) respectively. Eggs obtained from females that emerged in group A were incubated at 15, 18, 20, and 23°C, while those obtained from females of group B were used at 25, 30 and 35°C. Eggs were observed daily for 60 days to monitor the incubation period. After egg hatching, the neonate larvae were carefully removed with a fine camel hair brush and transferred into plastic containers (3.5 cm depth x 3.9 cm diameter) containing an artificial diet (see Gichuhi *et al.*, 2017, for diet preparation). The eggs that did not hatch were observed for an additional two months, after which they were recorded as dead. We kept the neonate larvae individually to avoid cannibalism and the diet was changed monthly. Three months after hatching, the larvae were transferred into bigger plastic containers (6.5 cm depth x 11.5 cm diameter) with approximately a 2 cm layer of artificial diet. The individuals were checked daily to monitor the moult to pupa stage as well as mortality. After pupation, the pupae were placed in a plastic container of the same size lined with a paper towel and monitored daily until adults emerged.

2.3. Reproduction and adult longevity

After emergence, adults were kept in the same temperatures as those used for immature stages to assess the fecundity and longevity at each constant temperature. Adults were placed individually in plastic containers (6.5 cm depth x 11.5 cm diameter) with coffee leaves and twigs as food, for the period of physiological and sexual maturation, as described by Gichuhi *et al*. (2017). Once the female began to feed, i.e. after four weeks on average, it was introduced into a polyethylene terephthalate bottle (2 litters in volume) with a male for mating. The bottles were cut from the top and then covered with a fine muslin cloth (0.1 µm) fixed with a rubber band to keep the adults inside. The bottles contained freshly cut coffee sticks (25 cm long) for feeding and egg laying slightly buried in moist soil. The sticks were checked daily to record the number of eggs laid by

each female. The sticks were changed every three days and survival of both males and females was monitored and recorded to assess longevity.

2.4. Model development

The Insect Life Cycle Modeling software (ILCYM version 3.0) (Tonnang *et al*., 2013) is an open source software built on two computer programs, Java and R (R Core Team, 2012). The software contains a model builder module that helps to develop temperature-dependent models for survival, development and reproduction (Tonnang *et al*., 2013). The model builder module contains a library of several empirical linear and nonlinear models proposed to describe the effect of temperature on the insect's development. The best-fitted models were selected based on the coefficient of determination (R^2) and Akaike's Information Criterion (AIC) (Tonnang *et al*., 2013), combined with the biological traits for *M. leuconotus* (i.e. the range of temperature in which the insect can develop). The software also allows the simulation of standard life table parameters according to temperature through a compilation of the different models.

2.4.1. Development time for immature stages and adult longevity

The distribution of insect development time is usually skewed (Sharpe & DeMichele, 1977). Thus, the development time of *M. leuconotus* immature stages and adult longevity measured at different constant temperatures were first normalised using ln-transformation and then fitted to cumulative density functions. . The cumulative frequency was plotted against ln-transformed development time in parallel lines, by fitting logit function for egg, larva, pupa and the adult male. The complementary log-log (CLL) function gave a better fit for the adult female longevity. The mathematical expressions of these functions are given below:

Logit distribution function: $F(x) = 1/(1 + \exp(-(a_i + b \ln x)))$

CLL distribution function: $F(x) = 1 - \exp(-\exp(a_i + b \ln x))$

where $F(x)$ is the probability of the life stage to complete its development at time x, $\ln x$ is the normalised development times (in days), a_i is the intercept corresponding to temperature i and b is the common slope of the model (Tonnang *et al*., 2013).

2.4.2. Development rate for immature stages

Both linear and nonlinear models were used to predict the impact of temperature on the development rate for *M. leuconotus* immature stages. In the first step, the development rate of each immature stage was calculated by inverting the median development time (1/median development time) and then plotted against temperature. Afterwards, a linear model was fitted to the development rate data. Using parameters of the linear model, the minimum temperature threshold (T_{min}) and the thermal constant (k, in degree days) were estimated as follow:

Linear model: $r(T) = a + bT$

Minimum temperature threshold: $T_{min} = -a/b$

Thermal constant: $k = 1/b$

where, $r(T)$ is the development rate at temperature T and a and b are the intercept and slope of the regression model, respectively, and k is the thermal constant in degree days.

However, the linear model cannot correctly predict the impact of temperature on development rate at extreme temperatures due to the nonlinearity of the relationship, as demonstrated for egg development in the present study. Hence, several nonlinear models were fitted and the best one selected based on the selection criteria (R^2 and AIC). Among fifty-nine models, the Logan model

(Logan *et al*., 1976) was the best for the development rate of all immature stages. The mathematical equation for the model is given below:

Logan model: $r(T) = \Upsilon \left\{ \exp(\rho T) - \exp\left(\rho\, T_{max} - \frac{(T_{max} - T)}{v}\right) \right\}$

where $r(T)$ is the development rate at temperature T, Υ is a measurable development rate at an arbitrary base temperature above developmental threshold, ρ is a composite Q10 value for enzyme-catalyzed biochemical reactions, T_{max} is the maximum lethal temperature and v is the width of the decline phase in development rate above the optimum temperature (Logan *et al*., 1976).

2.4.3. Mortality rate for immature stages

The mortality rate was calculated for each immature stage at each constant temperature and fitted to forty-five nonlinear models. Based on R^2 and AIC, Wang 1 model (Wang *et al*., 1982) gave the best fit for egg and pupa mortality rate. The polynomial function of degree 4 gave the best fit for the larval mortality rate. The mathematical equations of the models are given below:

Wang 1 model: $m(T) = 1 - \frac{1}{\exp\left(\left(1+\exp\left(-\frac{T-T_{opt}}{B}\right)\right)\times\left(1+\exp\left(-\frac{T_{opt}-T}{B}\right)\right)\times H\right)}$

Polynomial function of degree 4: $m(T) = \exp(b_1 + b_2 * T + b_3\sqrt{T})$

Where, $m(T)$ is the mortality rate at temperature T; T_{opt}, B and H are the Wang 1 model parameters; and b_1, b_2 and b_3 are polynomial function parameters (Tonnang *et al*., 2013).

2.4.4. Female fecundity and adult senescence

A modified exponential model of degree 1 described age-specific fecundity, which refers to the cumulative proportion of egg production in relation to the age of the females. The cumulative

oviposition rate was plotted against normalised female age expressed as a ratio of age in days divided by median survival time. Age specific fecundity was computed using the formula:

$$F(x) = 1 - \exp -(aT + bT^2 + cT^3)$$

Where, $F(x)$ is the cumulative oviposition frequency at the normalised female age x; T is temperature; *a*, *b* and *c* are the model parameters (Tonnang *et al*., 2013).

The mean oviposition rate per female was calculated for each constant temperature as the total number of eggs laid by the females divided by the total number of females. Then, the below polynomial function of degree 12 was fitted to describe the relationship between temperature and oviposition:

$$F(T) = \exp\left(b_1 + b_2 T + b_3 \log(T)\right)$$

Where, $F(T)$ is the mean female fecundity at temperature T; b_1, b_2 and b_3 are the model parameters (Tonnang *et al*., 2013).

Senescence is a decline in organism fitness due to ageing and it is used to assess demographic parameters such as longevity and fecundity (Boggs, 2009). In ILCYM, the terminology senescence is used for the adults rather than mortality to differentiate it from immature stage mortality (Tonnang *et al*., 2013). The adult senescence was calculated as the inverse of median longevity for both sexes (male and female) at each constant temperature and then plotted against temperature. Afterwards, Stinner 4 model (Stinner *et al*., 1974) was fitted to describe the relationship between temperature and female senescence. On the other hand, Hilbert and Logan 3 model (Tonnang *et al*., 2013) gave the best fit for the male senescence. The following mathematical expressions were used:

Stinner 4 model: $s(T) = \frac{C_1}{1+\exp(k_1+k_2 T)} + \frac{C_2}{1+\exp\left(k_1+k_2(2T_o-T)\right)}$

Hilbert and Logan 3: $s(T) = \Psi\left(\frac{(T-T_{min})^2}{(T-T_{min})^2+D} - \exp -\frac{\left(T_{max}-(T-T_{\min})\right)}{Dt}\right) + \theta$

Where, $s(T)$ is the senescence rate at temperature T; C_1, C_2, k_1, k_2 and T_o are Stinner 4 model parameters; Ψ, T_{min}, T_{max}, D, Dt and θ are Hilbert and Logan 3 model parameters.

2.4.5. Simulation of life table parameters

Life table parameters were simulated for different temperatures using the "stochastic simulation" in ILCYM, which is based on the rate summation and cohort up-dating approach (Curry et al., 1978). Validation and simulation modules ILCYM compiles all the models for the development time, development rate, mortality, fecundity, and adult senescence and uses them to simulate the life table parameters. The purpose of the simulation was to determine the thermal limits of *M. leuconotus* population growth and to establish how an increase in temperature affects population growth capacity. The estimated parameters include: 1) the intrinsic rate of natural increase (r_m) that determines the ability of a population to grow under specific ecological conditions, 2) the gross reproductive rate (*GRR*), which is known as the average number of daughters produced by a female throughout her lifespan, 3) the net reproductive rate (R_o), which is similar to *GRR* but takes into account the mortality rate of immature stages, 4) the mean generation time (*Tc*), which is the average time between the birth of parents and that of offspring, and 5) the doubling time (*Dt*), which is the time required for the population to double (Tonnang *et al*., 2013). For the simulations, the sex ratio was set at 0.5 (Tapley, 1960; Gichuhi *et al*. 2017). Simulations started with 150 individuals at the egg stage and were conducted for thirteen constant temperatures, from 20 to 32°C, with 1°C interval. The simulations were replicated three times for each temperature, bringing the number of runs to 450 individuals at egg stage.

2.5. Statistical analyses

The effect of temperature on the development time of *M. leuconotus* immature stages (in days) and adult longevity (in days) were both modelled with the Generalised Linear Model (GLM) procedure in R (R Core Team, 2016), with a Poisson distribution as recommended by O'Hara and Kotze (2010). Once significant differences were detected, the means were separated using Tukey test at $\alpha = 0.05$. Every life table parameter (intrinsic rate of increase, gross reproduction rate, net reproduction rate, mean generation time, doubling time and the finite rate of increase) obtained from the simulations were also separately modelled as a function of temperature, with the analysis of variance procedure (ANOVA) in R (R Core Team, 2016).

3. Results

3.1. Immature stage development time and adult longevity

Temperature had a significant effect on *M. leuconotus* development time and adult longevity ($P < 0.0001$) (Table 1). However, for all immature stages, development times at 23 and 25°C were not significantly different. Egg successfully developed to the larval stage at all tested temperatures in the range of 15-35°C. The incubation period was affected by temperature ($\chi^2 = 378.05$, $df = 371$, $P < 0.0001$), with values between 10.8 to 44.8 days, for 30 and 15°C, respectively (Table 1). Among immature stages, larva had the longest development time within the range from 194.2 to 543.1 days, for 30 and 18°C, respectively. The longest development time for the pupal stage was 48.6 days at 18°C and the shortest was 17.7 days at 30°C. Average female longevity was longest at 20°C with 168.3 days, compared to 116.0 days for the male at 25°C. The development time frequency distributions for egg, larva, pupa and the adult male were well described by logit models ($R^2 = 0.94$-0.98, AIC = 455.3-1189.2) (Table 2; Supplementary 1). The longevity frequency

Table 1. Immature stage development time and adult longevity (mean ± SD) for populations of *Monochamus leuconotus* reared at different constant temperatures in the laboratory. N is the total number of eggs used for the experiment at each constant temperature and *n* is the number of each life stage used to calculate the mean

T (°C)	N	Immature stage development time (days)						Adult longevity (days)			
		n	Egg	*n*	Larva	*n*	Pupa	*n*	Female	*n*	Male
15	50	30	44.80 ± 6.31a	30	-		-		-		-
18	76	63	29.17 ± 6.50b	22	543.05 ± 113.10a	15	48.60 ± 8.08a	8	154.00 ± 31.01a	7	38.57 ± 15.12a
20	100	71	22.37 ± 6.52c	42	408.48 ± 108.45b	35	41.50 ± 8.23b	18	168.28 ± 58.15a	17	94.31 ± 64.96b
23	85	72	15.88 ± 1.77d	39	292.89 ± 49.67c	37	29.08 ± 4.39c	16	135.63 ± 27.34b	21	99.23 ± 60.00c
25	81	67	14.28 ± 4.11d	42	285.86 ± 46.96c	35	26.03 ± 4.21cd	17	113.53 ± 31.49c	18	116.00 ± 49.99d
30	92	61	10.77 ± 2.43e	27	194.15 ± 25.66e	19	17.68 ± 2.67e	10	79.00 ± 18.44d	9	85.00 ± 31.42e
35	53	14	12.71 ± 1.81de	14	-		-		-		-
χ^2			378.05		172.15		125.17		68.11		64.56
d.f.			371		167		136		64		66
P-value			< 0.0001		< 0.0001		< 0.0001		< 0.0001		< 0.0001

Means in each column followed by the same letter are not significantly different (Tukey's HSD, $P = 0.05$).

Table 2. Statistics of the goodness of fit and parameters estimated for logit and complementary log-log (CLL) functions (*a* = y-intercept, *b* = common slope), fitted to cumulated frequency distributions for immature stage development time and adult longevity for populations of *Monochamus leuconotus* reared at different constant temperatures in the laboratory.

Model parameters (mean ± SE)	Immature stage development time				Adult longevity	
	Temperature (°C)	Egg	Larva	Pupa	Female	Male
Intercept (*a*) at:	15	-26.15 ± 0.59	-	-	-	-
	18	-23.12 ± 0.51	-52.86 ± 1.04	-39.04 ± 0.98	-22.54 ± 0.66	-10.42 ± 0.32
	20	-21.24 ± 0.48	-50.56 ± 0.99	-37.47 ± 0.93	-23.48 ± 0.69	-12.28 ± 0.37
	23	-18.82 ± 0.43	-47.62 ± 0.94	-33.89 ± 0.85	-22.07 ± 0.65	-13.13 ± 0.40
	25	-18.04 ± 0.41	-47.59 ± 0.94	-32.73 ± 0.82	-21.20 ± 0.62	-13.67 ± 0.41
	30	-16.07 ± 0.37	-44.23 ± 0.87	-28.90 ± 0.73	-19.47 ± 0.57	-12.81 ± 0.39
	35	-18.05 ± 0.42	-	-	-	-
Slope (*b*)		6.95 ± 0.15	8.43 ± 0.17	10.17 ± 0.25	4.45 ± 0.13	2.96 ± 0.09
R^2		0.94	0.95	0.98	0.91	0.94
AIC		949.06	1189.20	455.26	643.32	548.99

distribution for female fitted a CLL distribution (larva: R^2 = 0.91, AIC = 643.3) (Table 2; Supplementary 1).

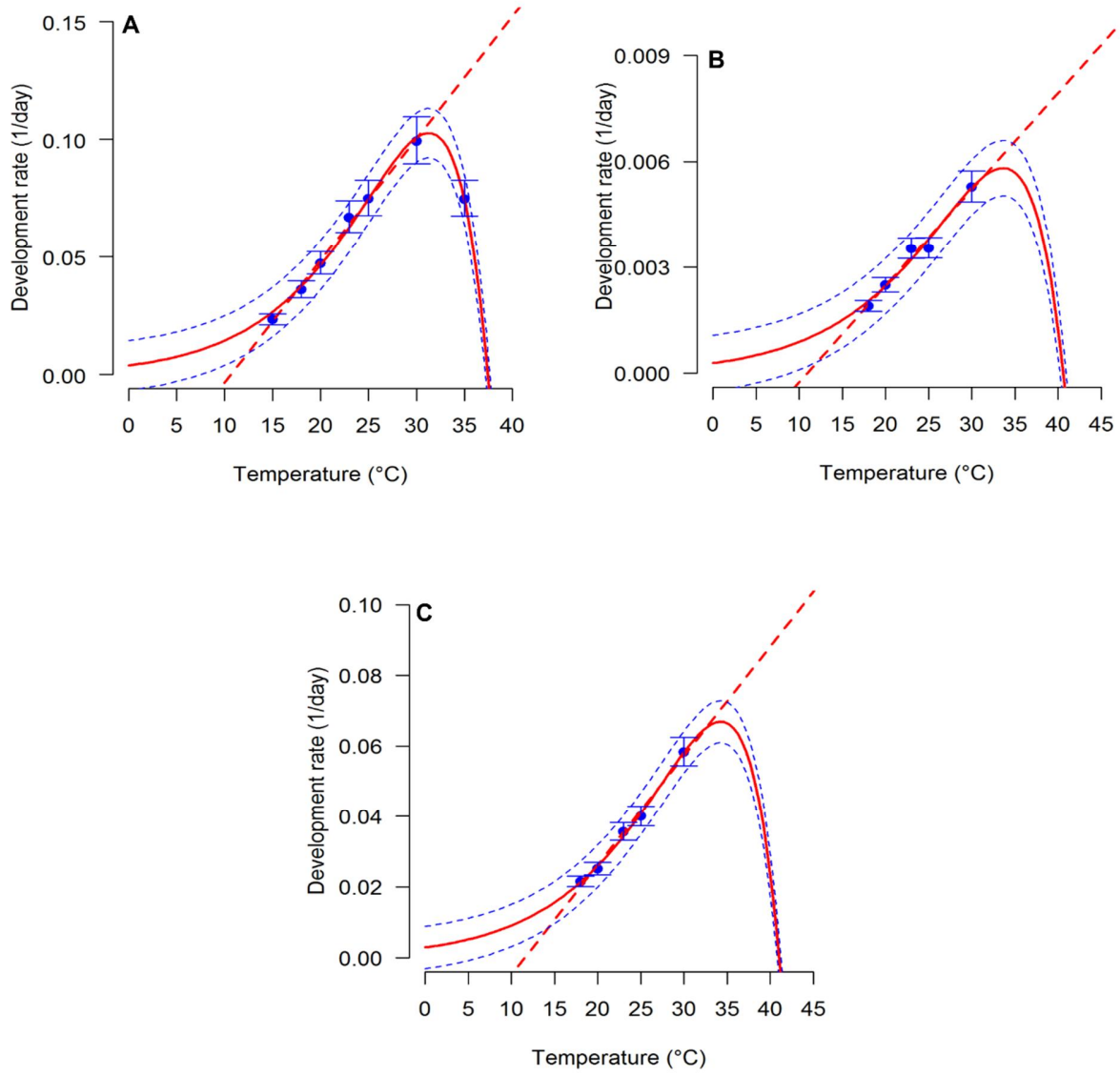

Fig.1: Model fitting to the relationship between the development rate of *Monochamus leuconotus* immature stages and temperature, with A) egg, B) larva and C) pupa. The blue points are the observed values with bars representing the standard deviation. Fitted models are the dashed straight lines for linear models and solid lines for the Logan models. Dashed lines in blue above and below represent the upper and lower 95% confidence interval.

Table 3. Statistics of the goodness of fit and parameters of models fitted to the relationship between development rate of *Monochamus leuconotus* immature stages and temperature, *F*: F-test statistic, *d.f.*: degree of freedom, *p*: probability value, R^2: coefficient of determination, and AIC: Akaike's Information Criterion.

Life stage	Model name	Model parameters (± SE)		Statistics				
				F	*d.f.*	*P*	R^2	AIC
Egg	Logan	Υ	0.012 ± 0.002	124.62	3,3	0.001	0.99	-56.06
		T_{max}	37.428 ± 0.001					
		ρ	0.158 ± 2.440					
		v	5.961 ± 0.020					
Larva		Υ	0.0004 ± 0.000	42.19	3, 11	< 0.001	0.92	-50.31
		T_{max}	40.643 ± 0.026					
		ρ	0.129 ± 0.001					
		v	6.356 ± 0.144					
Pupa		Υ	0.003 ± 0.001	88.85	3, 11	< 0.001	0.96	-29.70
		T_{max}	41.01 ± 0.009					
		ρ	0.122 ± 0.000					
		v	5.672 ± 0.207					

3.2. Immature stage development rate

Thermal parameters were estimated for every immature stage from the linear model fitted to the relationship between development rate and temperature (Fig.1). The minimum temperature threshold for development (T_{min}) was estimated at 10.7, 10.0 and 11.5°C, for egg, larva and pupa, respectively. The thermal constant was 192.3, 3333.3 and 322.6 degree days, for egg, larva and pupa, respectively. Fitting of linear model was good, with R^2 ranging between 0.97 and 0.99, and AIC between -66.39 and -46.85. For extreme temperature, the Logan model gave the best fit for all immature stages (R^2 between 0.92 and 0.99, and AIC between −56.06 and −29.70) (Fig.1; Table 3). The maximum temperature threshold (T_{max}) for egg, larva and pupa development was estimated from the model at 37.4, 40.6 and 41.0°C, respectively.

3.3. Immature stage mortality rate

Temperature had a significant effect on the mortality rate of *M. leuconotus* immature stages ($P \leq 0.05$) (Fig.2; Table 4). The temperature-dependent mortality of egg and pupa stage was well described by the Wang 1 model (R^2 = 0.91-0.93 and AIC between −13.04 and −13.76). A polynomial function of degree 4 gave the best fit for the larval stage (R^2 = 0.97 and AIC = −16.92) (Fig.2; Table 4). The optimum temperature for *M. leuconotus* immature stage survival was estimated from the models between 23.0 and 23.9°C. The larva stage did not survive at 15 and 35°C (Fig.2B) and showed the highest mortality when compared with egg and pupa, with a mortality of 65, 40, 45, 39 and 54% at 18, 20, 23, 25 and 30 °C, respectively.

Table 4. Statistics of the goodness of fit and parameters of models fitted to the relationship between the mortality rate of *Monochamus leuconotus* immature stages and temperature. *F*: F-test statistic, *d.f.*: degree of freedom, *p*: probability value, R^2: coefficient of determination, and AIC: Akaike's Information Criterion.

Life stage	Model name	Model parameters (± SE)		Statistics				
				F	*d.f.*	*P*	R^2	AIC
Egg	Wang 1	T_{opt}	23.019 ± 0.607	27.072	2,4	0.005	0.93	-13.76
		B	3.588 ± 0.421					
		H	0.044 ± 0.009					
Larva	Polynomial function 4	b_1	19.668 ± 1.748	69.710	2,4	< 0.001	0.97	-16.92
		b_2	0.857 ± 0.075					
		b_3	-8.393 ± 0.733					
Pupa	Wang 1	T_{opt}	23.972 ± 0.326	11.433	2,2	0.050	0.91	-13.04
		B	2.337 ± 0.374					
		H	0.026 ± 0.008					

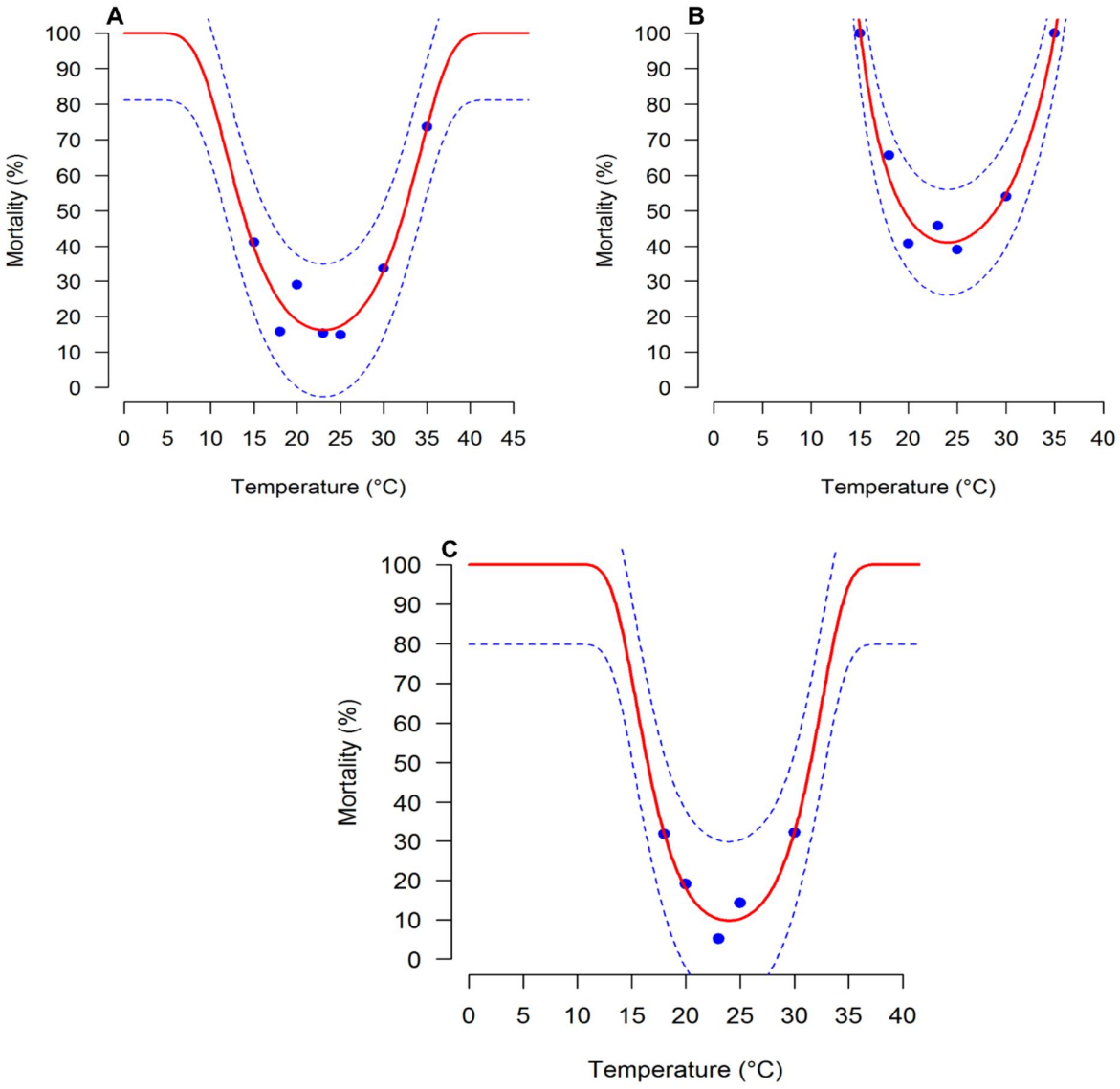

Fig.2: Model fitting to the relationship between the mortality rate of *Monochamus leuconotus* immature stages and temperature for A) egg, B) larva and C) pupal stages. The blue points are the observed values. Solid red lines are the fitted models: Wang 1 model for egg and Pupa, and polynomial function of degree 4 for larva. Dashed lines in blue above and below represent the upper and lower 95% confidence interval.

3.4. Female fecundity and adult senescence

Temperature significantly influenced female fecundity in *M. leuconotus* (Fig.3; Table 5). The exponential modified 1 model gave the best fit to the age-specific cumulative oviposition rate (R^2 = 0.97 and AIC= −2752.9). Fecundity was lowest at 30°C, with 38.7 eggs per female, whereas the highest fecundity was at 23°C, with 97.81 eggs per female (Fig.3B). The polynomial function of degree 12 gave the best fit to the relationship between *M. leuconotus* female fecundity and temperature (R^2 = 0.96 and AIC= 36.68) (Fig.3B; Table 5). The model showed that females of *M. leuconotus* might be able to lay eggs under temperatures between 11 and 40°C, with a maximum fecundity at around 23°C (Fig.3B; Table 5). The adult senescence of both males and females was significantly affected by temperature ($P < 0.05$). The Stinner 4 model described the impact of temperature on *M. leuconotus* female senescence (R^2 = 0.78 and AIC= −33.53) (Fig.3C; Table 5), whereas Hilbert and Logan 3 model gave the best fit for the male senescence (R^2 = 0.71 and AIC= −20.42) (Fig.3D; Table 5).

Table 5. Statistics of the goodness of fit and parameters of models fitted to describe the relationship between *Monochamus leuconotus* cumulative oviposition, mean total oviposition and adult senescence and temperature. *F*: F-test statistic, *d.f.*: degree of freedom, *p*: probability value, R^2: coefficient of determination, and AIC: Akaike's Information Criterion.

Demographic parameters	Model name	Model parameters (± SE)		Statistics				
				F	*d.f.*	*P*	R^2	AIC
Relative oviposition	Exponential modified 1	a	-0.243 ± 0.050	17360.0	2,818	< 0.001	0.97	-2410.9
		b	2.451 ± 0.177					
		c	-0.120 ± 0.143					
Mean total oviposition	Polynomial function 12	b_1	-43.639 ± 8.285	25.13	2,2	0.038	0.96	36.68
		b_2	-1.004 ± 0.173					
		b_3	22.733 ± 3.913					
Female senescence	Stinner 4	C_1	4.036 ± 0.628	8.86	4,10	0.002	0.78	-33.53
		C_2	0.084 ± 0.052					
		k_1	4.826 ± 0.292					
		k_2	0.129 ± 3.065					
		T_o	2.792 ± 0.020					
Male senescence	Hilbert and Logan 3	Ψ	994025.5 ± 0.000	4.39	5,9	0.026	0.71	-20.42
		T_{min}	25.899 ± 0.564					
		T_{max}	38.567 ± 0.000					
		D	313420808 ± 0.000					
		Dt	0.017 ± 0.000					
		θ	0.008 ± 0.002					

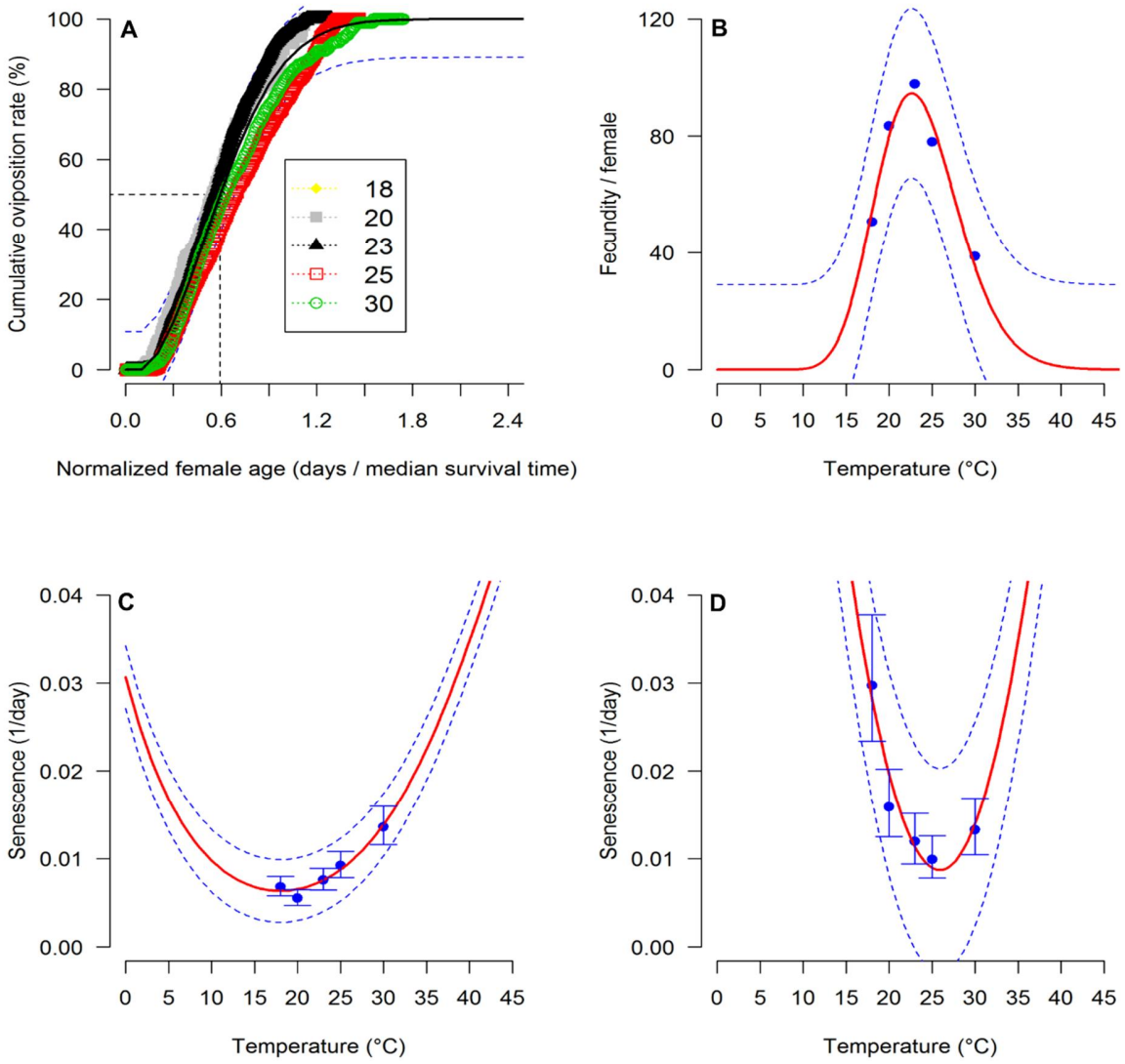

Fig.3: Model fitting to the relationship between fecundity in *Monochamus leuconotus* female and temperature, and adult senescence and temperature: A) cumulative oviposition fitted to exponential modified 1 model; B) average fecundity of the females fitted to polynomial function 12; C) female senescence rates fitted to Stinner 4 model and D) male senescence rates fitted to Hilbert and Logan 3 model. The blue points are the observed values with bars representing the standard deviation. The solid red lines are the fitted models with dashed lines in blue above and below representing the upper and lower 95% confidence interval.

Table 6. Simulated life table parameters (mean ± SD) of *Monochamus leuconotus* populations reared at different constant temperatures (number of eggs used for the simulation = 150). r_m: intrinsic rate of natural increase, *GRR*: gross reproduction rate, R_o: net reproduction rate, *Tc*: mean generation time, D_t: doubling time, and λ: finite rate of increase.

T (°C)	r_m	*GRR*	R_o	*Tc*	D_t	λ
20	-0.008 ± 0.001	0.58 ± 0.44	0.05 ± 0.02	363.01 ± 0.99	-	-
21	-0.001 ± 0.002	2.30 ± 0.97	0.86 ± 0.42	352.51 ± 1.06	-	-
22	0.002 ± 0.001	5.07 ± 3.05	2.31 ± 1.39	342.54 ± 9.70	245.36 ± 98.48	1.003 ± 0.001
23	0.005 ± 0.000	9.95 ± 0.98	4.96 ± 0.32	333.85 ± 8.92	144.86 ± 9.26	1.005 ± 0.000
24	0.007 ± 0.001	20.26 ± 2.14	9.41 ± 2.20	321.57 ± 4.54	100.79 ± 8.64	1.007 ± 0.001
25	0.007 ± 0.001	26.32 ± 4.71	10.59 ± 1.75	315.36 ± 2.69	93.41 ± 7.87	1.007 ± 0.001
26	0.008 ± 0.001	34.60 ± 8.59	11.81 ± 2.50	308.64 ±11.34	87.95 ± 11.68	1.008 ± 0.001
27	0.008 ± 0.000	40.91 ± 3.96	11.16 ± 2.35	285.19 ± 11.89	82.81 ± 4.96	1.008 ± 0.000
28	0.008 ± 0.001	35.79 ± 12.89	8.23 ± 3.16	256.33 ± 32.89	87.21 ± 11.67	1.008 ± 0.001
29	0.007 ± 0.000	40.57 ± 14.57	6.69 ± 1.04	264.21 ± 4.42	97.13 ± 6.60	1.007 ± 0.000
30	0.004 ± 0.002	25.38 ± 9.04	3.15 ± 1.36	254.15 ± 2.79	197.24 ± 112.61	1.004 ± 0.002
31	0.001 ± 0.000	15.92 ± 4.38	1.15 ± 0.01	237.95 ± 1.74	-	-
32	-0.004 ± 0.004	8.67 ± 8.90	0.56 ± 0.42	223.90 ± 18.71	-	-
F	41.01	12.09	20.06	42.01	59.24	12.96
d.f.	12, 25	12, 25	12, 25	12, 25	9, 17	9, 17
p	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001

3.5. Life table parameters

Temperature had a significant effect on the simulated life table parameters of *M. leuconotus* ($P < 0.0001$) (Table 6). The intrinsic rate of natural increase r_m was maximal between 26 and 28°C, with a value of 0.008, and negative at 20, 21 and 32°C. The highest *GRR* was at 27°C, with 40.9 daughters per female, whereas the lowest was at 20°C, with 0.58 daughters per female. The net reproductive rate R_o ranged from 0.05 daughters per female per generation at 20°C, to 11.8 daughters per female per generation at 26°C. The mean generation time *Tc* decreases with an increase in temperature, with the longest time (363 days) at 20°C, and the shortest (223.9 days) at 32°C. The time required for the population to double (D_t) was minimal at 27°C, with 82.8 days, and maximal at 22°C, with 245.4 days. The highest finite rate of increase λ was at temperatures between 26 and 28°C, with a value of 1.008, whereas the shortest was 22°C, with a value of 1.003 (Table 6).

4. Discussion

4.1. Colony initiation and rearing method

In this study, we provided the first description of the impact of temperature on the development, survival and reproduction of the African coffee white stem borer, *Monochamus leuconotus*. Previous studies on the biology of this important pest were either carried out on coffee trees in the field (Knight, 1939; Tapley, 1960) or in the laboratory, by observing immature development in coffee stems (Schoeman *et al*., 1998). For the first time, Gichuhi *et al*. (2017) provided both an innovative rearing method using an artificial diet for larvae and coffee sticks for oviposition, and basic information on the life cycle and behavior of this important pest of coffee. In the present study, we used the first generation of *M. leuconotus* obtained by Gichuhi *et al*. (2017) to start our

colony. Built on the rearing method of the same authors, we obtained at five constant temperatures a complete life cycle and data for survival and fecundity for the second generation of *M. leuconotus* maintained in the laboratory. This allowed us to provide the pest thermal requirements and simulate the life table parameters. However, in order to be able to observe individuals for their all life, from egg incubation to oviposition, some improvements were made to the rearing method. Eggs were early extracted from the bark and kept in wet conditions for observation throughout the incubation period. Adults were kept on coffee sticks in 2-liter polyethylene bottles, big enough to allow pairs to mate and female oviposition in good conditions, but small enough to be stored in good numbers in incubators.

4.2. Life cycle

4.2.1. Oviposition and egg development

Our study showed that *M. leuconotus* females needed approximately one month after emergence for physiological and sexual maturation. This confirms the results obtained by Gichuhi *et al.* (2017). An observation that was not reported by these authors is an aggressive behaviour of males facing sexually immature females, usually leading to amputation of female legs and antennae. This behaviour might reflect male confusion between immature females and competitor males. At 25°C, with around 78 eggs per female, oviposition was twice higher than that reported by Knight (1939) and Gichuhi *et al*. (2017), with around 40 eggs per female. Our results are more in line with the records of Schoeman *et al*. (1998), who reported an average of 80.5 eggs per female at 26°C in field conditions.

By early extracting eggs from the bark and keep them in a moist environment, we increased egg hatchability by 47%, when compared to that obtained by Gichuhi *et al*. (2017), who kept eggs in

the bark until larvae emerged. In cerambycids, the moisture level in plant tissues is known as a crucial factor that determines egg hatchability (Hanks, 1999). The incubation period we obtained at 25°C (14.3 days) is in line with that of Schoeman *et al.* (1998), who reported an incubation period of 15 days at 26°C. However, it differs from records of Gichuhi *et al*. (2017), who obtained 26.6 days at 25°C. Under field conditions, Tapley (1960) recorded an incubation period between 21 and 23 days. Again, variation in egg development time may be related to rearing and observation methods.

4.2.2. Larval and pupal development

The average development time for the larval stage ranged from 194.2 to 543.1 days in the temperature range 18-30°C. Overall, this was shorter than records of Tapley (1960), who reported 600 days when the larvae were maintained in coffee stems. The use of an artificial diet might have accelerated larval development because of better nutritional properties in comparison to coffee wood (Gichuhi *et al*., 2017). By contrast, the pupal development time at 25°C was more constant and similar to the records of Schoeman *et al.* (1998) and Gichuhi *et al*. (2017).

Larval development was surprisingly variable in our study, especially for individuals reared in homogeneous conditions of food, temperature, humidity and photoperiod. For example, the duration of the larval stage ranged between 330 and 751 days at 18°C. Similar variation was observed by Gichuhi *et al*. (2017) for the first generation of *M. leuconotus* reared on an artificial diet. Intraspecific variability in larval development time has been observed for many insects. It can be explained by a variation in the number of larval instars or by a variation of the duration of one or several instars, or by both of them (Esperk *et al*, 2007). In our study, we did not observe moulting in order to limit disturbance during larval development. However, an additional larval instar (from

7 to 8) is a strong hypothesis for *M. leuconotus*, as it has been observed in other cerambycids, including in species of the genus *Monochamus* (Esperk *et al*., 2007). In nature, *M. leuconotus* adults emerge following a pattern with two peaks in the year, in March-May and September-November, which match the two rainy seasons of the rainfall pattern in coffee production areas of East Africa (Tapley, 1960; Schoeman *et al*., 1998; Liebig *et al*., 2018). Our hypothesis is that the variation in the larval development may be an adaptation to avoid the emergence of all the adult population at the same time in the year in order to limit the risk of failing reproduction due to sub-optimal environmental conditions.

4.3. Temperature-dependent development models

4.3.1. Development models

In nature, insects do not develop at constant temperatures. However, development modelling using data obtained at constant temperatures in the laboratory provides useful information on the pest development in relation to temperature such as thermal requirements. In addition, these models are often used to understand and *predict* insect distribution as impacted by temperature (Tonnang *et al*., 2013; Azrag *et al*., 2018). Here, we provided the thermal response curves for *M. leuconotus* development rate, fecundity, mortality, and adult longevity, also known as thermal reaction norm. Despite the fact that the thermal reaction norm for an insect usually has a complex shape, the appropriate model that describes it should be based on the unimodal shape that predicts the minimum, the optimal, and the maximum temperature thresholds (Régnière *et al*., 2012). Taking this into consideration, the models developed in this study were appropriate and well described the thermal reaction norm of *M. leuconotus*. The Logan model (Logan *et al*., 1976) that considers enzyme-catalyzed biochemical reactions rate for insect at the optimum temperature predicted well

the development rate of *M. leuconotus*. This standard model for insect development was previously used for many other species in tropical regions such as *Busseola fusca* F. and *Sesamia calamistis* H. (Khadioli *et al*., 2014), *Plutella xylostella* L. (Ngowi *et al*., 2017), and the coffee pest *Antestiopsis thunbergii* (Azrag *et al*., 2017). Similarly, other standard models used in our study were previously reported as appropriate to describe the relationships between insect demographic parameters and temperature (i.e. Sporleder *et al*., 2004; Fand *et al*., 2014; Soh *et al*., 2018)

4.3.2. Impact of temperature and thermal requirements

Oviposition and immature stage development were strongly impacted by temperature in our study. According to oviposition models, *M. leuconotus* females can lay eggs under temperatures in the range of 11-40°C. This may be considered as a wide range when compared to that of other insects sharing the same Arabica coffee plantations of the region. For example, for the coffee berry borer, *Hypothenemus hampei* Ferrari and the antestia bug, *Antestiopsis thunbergii* Gmelin, oviposition occurs in temperature range 15-32°C and 15-30°C, respectively (Jaramillo *et al*., 2009; Azrag *et al*., 2017).

The minimum temperature threshold (T_{min}) for immature stage development ranged between 10.0 and 11.5°C. The maximum temperature threshold (T_{max}) was predicted at 37.7, 40.6, and 41.0°C, for egg, larva and pupa, respectively. It should be noted that only a few larvae were obtained at 35°C and most of them died early, probably because of the quick drying up of the diet at this temperature. This constraint related to the rearing method might have interfered with temperature and somewhat skewed the thermal curve. Nevertheless, Logan model gave similar T_{max} values for other insect pests in Kenya, like the diamondback moth *Plutella xylostella* L., with 40.6, 40.7 and 38°C, for egg, larva, and pupa, respectively (Ngowi *et al*., 2017). Since the artificial diet might

have accelerated the larval development, it could also have an effect on the calculations of the thermal requirements and thermal constant. Therefore, these results should be considered with caution when exploiting such information to make a geographic prediction for *M. leuconotus*. Globally, we found larvae to be more susceptible to temperature in comparison with other life stages with a mortality rate between 39 and 100% at all tested temperatures. This is in contrast with records of Gichuhi *et al.* (2017) who reported 10% mortality at 25°C, and may reflect interference between temperature and other components of the rearing methods, such as the quality of artificial diet. In addition, whatever the temperature, we observed few larvae and adults with body deformation, which may be partly attributed to the inbreeding in the colony.

4.4. Simulation of life table parameters

This study is the first report of a demographic analysis for *M. leuconotus* and our results will help better understand the pest population dynamics in coffee plantations. However, as mentioned before, our rearing populations were maintained in conditions that do not reflect natural conditions, especially for the quality of food and exposure to extreme temperature and dryness. Thus, the results presented here should be considered as trends, as the simulated figures for life table parameters may differ from those of natural populations. Nevertheless, we found that the net reproductive rate (R_o) was the highest at 26°C, with 11.8 daughters per female. By taking into account immature stage mortality and sex ratio, this parameter characterises the growth rate (around 12), from one generation to the following, of our rearing populations (Ahmed *et al.*, 2016). The simulated intrinsic rate of natural increase (r_m), which is a synthetic parameter also indicating the capacity of the rearing population to grow, was maximal between 26 and 28°C, with a value of 0.008. This value is low when compared to report for *Monochamus galloprovincialis* (Olivier)

maintained in black pine logs in the laboratory, with a value of 0.05 at 24-26°C (Akbulut *et al*., 2007). *M. galloprovincialis* is a species from temperate countries that exhibits a life cycle by far shorter than that of *M. leuconotus* and this explains higher values for r_m. Nevertheless, in our rearing conditions, simulations showed that *M. leuconotus* populations could grow under temperatures ranging from 22 to 31°C. Outside this range, negative r_m values indicate populations decreasing with time. The simulated mean generation time reached a maximum value of around one year at 20°C and was between 250 and 300 days under temperatures in the range 26-28°C, which is the range for optimal population growth. By contrast, reports of field studies revealed that *M. leuconotus* needs between one year and half and two years to complete one generation (Knight, 1939; Tapley, 1960; Schoeman *et al*., 1998).

4.5. Conclusions and perspectives

Our study provides hitherto unreported temperature-dependent development models, as well as thermal requirements and demographic parameters of an important pest of Arabica coffee in east Africa highlands, the African coffee white stem borer *Monochamus leuconotus*. On one hand, we stressed the fact that our results were obtained under the specific conditions of a laboratory rearing at constant temperature and using an artificial diet as food for larvae. On the other hand, by improving our understanding of the relationships between the pest development and temperature, the trends presented in this paper will help understand population dynamics in coffee plantation and predict the risk for more efficient pest management, especially under climate warming. Finally, our study raised questions that should be answered in further studies in order to improve our global knowledge of insect life history and evolution. For example, the reason for the large variation in larval development time should be elucidated. We assumed that two population types

might have differentiated in nature in order to limit the risk of failing reproduction due to sub-optimal environmental conditions at adult emergence, one population with a short development time (one year and half) and one with a long development time (two years). Despite the value of such knowledge in the context of climate change, this kind of adaptation to climate seasonality and variability was rarely studied for tropical insect species and we strongly recommend further studies on *M. leuconotus* focused on this topic.

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