Temperature-dependent phenology of the parasitoid *Fopius arisanus* on the host *Bactrocera dorsalis*

Samuel Nanga Nanga [a,b,*], S. Kekeunou [b], A. Fotso Kuate [a], K.K.M. Fiaboe [a], M. A. Dongmo Kenfak [a], H.E. Tonnang [c], D. Gnanvossou [d], C. Djiéto-Lordon [b], R. Hanna [a,1]

[a] *International Institute of Tropical Agriculture (IITA), PO Box 2008, Messa Yaoundé, Cameroon*
[b] *Faculty of Science, University of Yaoundé I, PO Box 812, Yaoundé, Cameroon*
[c] *International Centre of Insect Physiology and Ecology (icipe), PO Box 30772, Nairobi, Kenya*
[d] *IITA-Benin, 08 BP 0932 Tri Postal, Cotonou, Benin*

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ABSTRACT

Fopius arisanus (Sonan), an egg-pupal parasitoid of numerous fruit fly species, was recently introduced into Africa for the control of the Oriental fruit fly, *Bactrocera dorsalis* (Hendel). In this study, life-table data of *F. arisanus* were generated under laboratory conditions at six constant temperatures (15, 20, 25, 30, 28 and 35 °C; 75% RH, L12:D12 photoperiod) and under variable conditions in a screenhouse on *B. dorsalis*. Several non-linear functions were fitted to model species development, mortality, longevity and oviposition using the Insect Life Cycle Modeling (ILCYM) software. The established phenology models were stochastically simulated at variable temperatures to estimate the life table parameters. *Fopius arisanus* completed development from egg to adult at all the temperatures tested except at 35 °C. Mean developmental time from egg to adult was inversely proportional to the temperature. The minimum temperature threshold (*Tmin*) from egg to adult was 8.15 °C, while the maximum temperature threshold (*Tmax*) was estimated at 34.2 °C. The optimal temperature for immature stages survival was predicted for 20–30 °C. The optimum fecundity estimated was 251 eggs/female at 22 °C. Following the stochastic simulations under natural conditions of the selected agro-ecological zones, it appears that the Humid Forest with Bimodal Rainfall provides a suitable thermal condition for potential population growth of *F. arisanus*. The present study shows the importance of temperature on the demographic parameters of *F. arisanus*. Implications of present findings on the biological control of *B. dorsalis* under climate change scenarios is discussed.

1. Introduction

Several tephritid fruit fly species are world-wide pests of major economic importance (White and Elson-Harris, 1992). In Africa, the invasive species *Bactrocera dorsalis* (Hendel) (Diptera: Tephritidae), initially described as *B. invadens* (Drew et al., 2005), has become the most important threat to fruit production on the continent, adding to losses caused by several native fruit fly species in the genera *Ceratitis* and *Dacus* commonly infesting fruits in Africa (San Jose et al., 2013; Schutze et al., 2015a, 2015b). *Bactrocera dorsalis* was first detected in Africa on the Indian Ocean coast of Kenya (Lux et al., 2003) and has since colonized 42 African countries, including the islands of Madagascar, Cape Verde, Comoros, and Mayotte (CABI, 2018; De Villiers et al., 2016). In

Africa, *B. dorsalis* infests over 40 cultivated and wild host plant species with up to 70% damage in cultivated fruits such as mango (*Mangifera indica* L.), guava (*Psidium guajava* L.) and citrus (*Citrus* spp. L.) (De Meyer et al., 2010; Goergen et al., 2011; Hanna et al., 2008a; Nanga et al., 2019). A range of control methods have been tested and implemented, singly or in combination, with a variable degree of success (Appiah et al., 2014; Ekesi and Billah, 2006; Hanna et al., 2008b; Muriithi et al., 2016; Van Mele et al., 2007).

Because of its exotic nature in Africa, classical biological control of *B. dorsalis* has been considered a highly desirable management option. Initial efforts focused on the co-evolved parasitoid *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae) which was introduced from Hawaii (USA) into Africa for evaluation and release for the control of *B. dorsalis*.

Fopius arisanus is a solitary egg-pupal endoparasitoid, originating in Asia, where it is found parasitizing eggs and first instar larvae of fruit flies (Altuzar et al., 2004; Bautista et al., 1998; Calvitti et al., 2002). Its larva develops as a parasite within the host larva until the latter reaches the pupal stage (Bautista et al., 2001; Moretti and Calvitti, 2003). Adults emerge a few days after the emergence of un-parasitized hosts. The parasitoid is known to parasitize numerous frugivorous tephritid fruit fly species, but predominantly *Bactrocera* species (Mohamed et al., 2010; Rousse et al., 2005; Zenil et al., 2004).

Since its introduction from Southeast Asia into Hawaii in the 1940s, *F. arisanus* has become the most successful natural enemy of *B. dorsalis* on the Hawaiian Islands (Haramoto and Bess, 1970). Successful control of *B. dorsalis*, *B. kirki* (Froggatt), and *B. tryoni* (Froggatt) has also been achieved more recently in French Polynesia following the introduction of *F. arisanus* into several islands (Vargas et al., 2007, 2012, 2013). Taken together, the association of *F. arisanus* with *Bactrocera* species and its realized impact on several *Bactrocera* species on Pacific islands have placed this parasitoid in the forefront of candidates for introduction into Africa for the classical biological control of *B. dorsalis*. In recent studies, Mohamed et al. (2010) documented over 70% parasitism of *F. arisanus* on *B. dorsalis* when reared on an artificial diet. Moreover, promising results have been reported in Benin where field releases resulted in up to 46% parasitism by the parasitoid on *B. dorsalis* infesting wild mango *Irvingia gabonensis* (Aubry-Lecomte) Baill (Gnanvossou et al., 2016; Mohamed et al., 2017). Nonetheless, attempts to introduce *F. arisanus* in other areas for suppression of fruit flies have failed including Mexico (1954), Peru (1960), and Argentina (1961) (Rendon et al., 2006), and the USA in Florida (1974) (Baranowski et al., 1993). It has been assumed that these failures were the result of several factors, with inadequate climate conditions being the most prominent (Calvitti et al., 2002; Larios et al., 2002; Rousse, 2007).

Climate has a strong effect on the distribution and abundance of insects (Damos and Savopoulou-Soultani, 2012), with temperature being the main driver of key functions of insects including development, survival, and reproduction (Rebaudo and Rabhi, 2018). In tri-trophic interactions between plants, herbivorous insects, and their natural enemies (predators, parasitoids, and pathogens), temperature changes may differently influence the biology of species in a given system, provoking a destabilization in their population dynamics that may lead to the extinction of part of the system (Hance et al., 2007; Van der Putten et al., 2004). Understanding the consequences of the thermal effects on all the interacting trophic levels, particularly on the third trophic level, is therefore of fundamental and applied importance, especially when using parasitoids in biological control programs (Harrington et al., 2001; Landsberg and Smith, 1992).

Previous studies on the thermal response of *F. arisanus* reared on *B. dorsalis* have been limited to a single constant temperature (Bautista et al., 1998; Vargas et al., 2002); variable ambient temperatures (Bautista et al., 1998); or a range of constant temperatures but only for immature development and adult longevity (Appiah et al., 2013). There is surprisingly little information on reproduction and population parameters of *F. arisanus* at a wide range of constant temperatures. Considering the enormous economic impact of *B. dorsalis*, the primary host of *F. arisanus*, on fruit production on four continents, it is imperative to quantify the effects of temperature on the life history of *F. arisanus* (with *B. dorsalis* as host) across a wide range of temperatures that the parasitoid would potentially experience in environments where it could be used for the biological control of *B. dorsalis*. Several approaches have been traditionally used to provide the aforementioned needed information, among them are temperature-driven phenology models that include a set of functions describing temperature-dependency (Fand et al., 2014; Khadioli et al., 2014; Mujica et al., 2017; Sporleder et al., 2017). This approach has become an important analytical tool for the evaluation, understanding, and prediction of the dynamics of insect populations in agroecosystems with the distinct advantage of its linkage to GIS module for predicting the establishment, activity, and growth of

the target insects in various environments. Such an approach is particularly useful for evaluating the response of the target insect to climate change (Sporleder et al., 2017).

The principal objectives of this study were therefore: (1) to develop a temperature-driven phenology model using a broad range of constant temperatures and variable conditions in a semi-natural environment, encountered by the parasitoid across its present range and (2) to validate the phenology model under a range of conditions representing regions where the parasitoid can be introduced for the biological control of *B. dorsalis*. We hypothesized that suitable thermal conditions or potential establishment area of the parasitoids will be closed to that of the host *B. dorsalis* and that its development parameters are likely to be affected by climate change.

2. Materials and methods

2.1. Host and parasitoid colony maintenance

A colony of *B. dorsalis* (100 males and 100 females) was initiated from individuals obtained from the incubation of mango fruits (var. Camerounaise) collected from IITA-Cameroon experimental orchard near Yaoundé, Cameroon (N 03.86406, E 011.46270 and 770 m). For *F. arisanus*, the individuals used in this study originated from the laboratory colony initiated from the population released in the IITA-Cameroon experimental orchard starting in 2010 and those emerging (approximately 100 pairs) from the incubation of mango and guava fruits collected from the orchard. The rearing techniques of both species followed those of Nanga et al. (2019).

2.2. Data collection

2.2.1. Experimental conditions

We carried out complete life table experiments from 2013 to 2014- in climate-controlled incubators (30-VL and 36-VL, Percival Scientific Inc., Perry, Iowa, USA) - to determine the effect of six constant temperatures (15, 20, 25, 30, 28, and 35 °C) on development, survival, and reproduction of *F. arisanus*. The parasitoid development has three larval instars inside the egg-larva of the host and one puparium stage (Rousse et al., 2005). In the case of this study, the parasitoid immature development was divided into the egg-larva stage of the parasitized host and the puparium stage of the parasitoid. The desired temperature and relative humidity (maintained at 65–75% across all temperatures) inside the incubators were logged at hourly intervals using HOBO Pro v2 Temp/RH (Onset Computer Corp., Boume, MA, USA). The photoperiod regime was kept at 12L:12D throughout all experiments. The temperatures were chosen to reflect a broad range of temperature environments that the parasitoid would experience in Africa and on other continents.

We also carried out two complete life table experiments during the wet and dry seasons under variable conditions in a screenhouse (Rossel Virology Screenhouse, Clovis Lande Ass. Ltd., Kent, UK) at the IITA Cameroon campus. The wet and dry season experiments were conducted respectively between August and October 2013 and between December 2013 and March 2014. Temperature and relative humidity in the screenhouse were logged at hourly intervals using HOBO Pro v2 data loggers (Onset Computing, MA, USA). The data are presented as daily averages from August 2013 through March 2014 (Fig. 1).

2.2.2. Development of immature stages and their survival

The parasitoid oviposition unit consisted of a dome (5-cm diameter) of ripe papaya fruit placed in a Petri dish (5.5 cm diameter). Five equidistant holes were perforated on the fleshy part of the dome using a 1-cm diameter corkborer, without damaging the epidermis. Three other small holes were punctured through the epidermis to facilitate the insertion of the female ovipositor. A papaya dome, with pulp removed, was exposed for 1–3 h to *B. dorsalis* females for egg collection. With the aid of a fine camel hair brush (size 3), 20 newly laid eggs were deposited
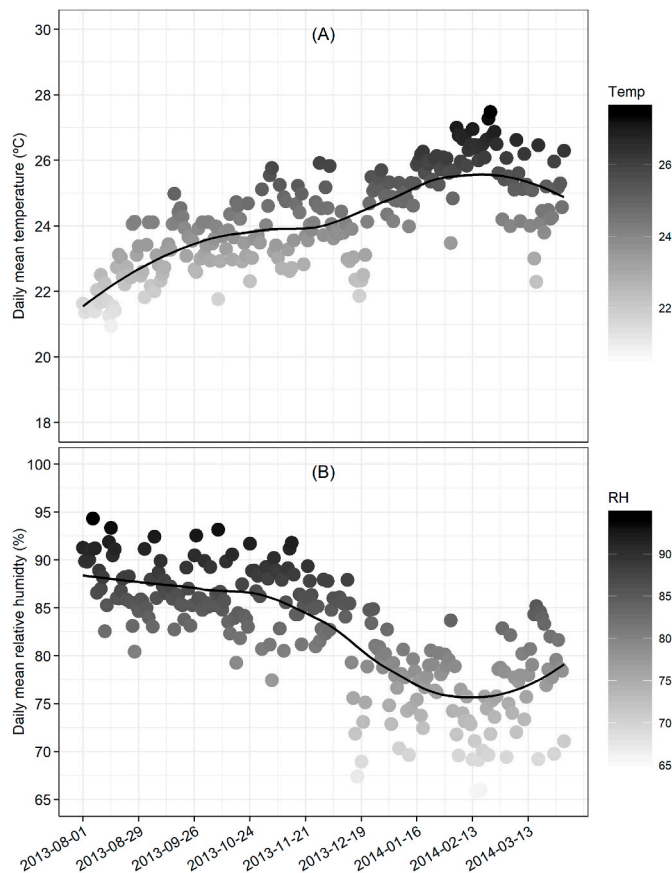
Fig. 1. Distribution of mean daily temperature (a) and relative humidity(b) in the screenhouse during the wet season (2013-08-01 to 2013-10-15) and dry season (2013-10-15 to 2014-03-1). Bold lines represent mean temperature (a) and mean relative humidity (b), while dots represent mean daily minimum and maximum temperature (a) and relative humidity (b) respectively.

on a small round, humidified tissue paper (1-cm diameter) placed on top of a piece of papaya (1-cm diameter, 10 mm long). Thereafter, the piece of papaya with these eggs was introduced into each hole of 1-cm diameter. Two oviposition units, each with 100 eggs, were then presented to 10 pairs of 7-day-old *F. arisanus* adults isolated in a 15 × 15 × 15 cm Plexiglas cage. Four replicate cohorts (i.e., 4 replications), each with 200 *B. dorsalis* eggs making a total of 800 eggs per temperature regime, were exposed for parasitism at each temperature regime. The oviposition units were maintained at room conditions (25 °C, 60–80% RH, and 12L:12D photoperiod). Twenty-four hours after exposure, a subsample of 3–6 randomly selected eggs from each hole was used to assess the initial parasitism rate using a modified dechorionating treatment (Moretti and Calvitti, 2003; Rousse, 2007). The eggs were immersed for 2 min in 2.6% NaCl water solution, then rinsed with distilled water and fixed onto a microscope slide in a droplet of glycerol to avoid desiccation during the examination. The slides were observed under a binocular microscope at 100x magnification. Cohorts with less than 20% parasitized eggs were discarded. The remaining eggs in each cohort were transferred to a 25-ml plastic cup (one egg per cup) containing 10 g of a carrot-based diet (Ekesi and Mohamed, 2011). The cups were labelled, covered with a piece of black cloth to prevent the hatched larvae from escaping, and transferred into incubation chambers set at the desired temperatures with RH maintained at 65–75% and a photoperiod of 12L:12D. Fully developed puparia were individually transferred into Petri dishes (9 cm diameter) and maintained under the same thermal conditions until emergence. Mortality and development time were recorded daily for each individual. The number of puparia, emerged adult *F. arisanus* and *B. dorsalis* and their sex, and un-hatched

puparia were also recorded. The un-hatched puparia were subsequently dissected to determine their status – empty puparia, unhatched fly host, or unhatched parasitoid. The percentage of recovered puparia, adult emergence, and empty puparia were computed. Longevity and reproduction were determined for emerged adult parasitoids. The same procedures used under constant temperatures were repeated in the two experiments at ambient, variable conditions in the screenhouse during the wet and dry seasons, but with 4 and 3 replicate cohorts of 200 eggs respectively in the wet and dry seasons experiments.

2.2.3. Adult longevity and reproduction

On the day of adult *F. arisanus* emergence, one female and one male were paired and placed in a 15 × 15 x 15-cm Plexiglas cage and provided with water and honey. Cages were then transferred into incubation chambers set at 15, 20, 25, 28, and 30 °C, as well as at variable conditions in the screenhouse for oviposition assessment. The temperature of 35 °C was excluded from further consideration as parasitoid development did not occur at this temperature. The sex ratio was female-biased; therefore, males from the stock colony were added to some cages for mating. Five days post-emergence, each adult female was provided with 20 newly laid eggs of *B. dorsalis* placed in an oviposition unit consisting of a round piece of ripe papaya fruit (3 cm diameter) in which a 1-cm diameter hole was perforated in the center of the fleshy part as described above. The unit was replaced daily until the death of the female parasitoid. After exposure, eggs were gently removed from the oviposition unit and the dechorionating treatment was used to assess daily oviposition (Moretti and Calvitti, 2003; Rousse, 2007). Adult longevity of females and males was also recorded for each constant temperature and under variable conditions in the screenhouse. Adult female pre-oviposition period (APOP), total pre-ovipositional period counted from egg to first oviposition (TPOP), and oviposition period were calculated accordingly. The number of adult pairs varied between 38 and 86 pairs at constant temperatures and between 27 and 64 pairs under variable conditions.

2.3. Phenology models

2.3.1. Modeling software

Temperature-dependent models or functions were used to model the demographic parameters of *F. arisanus* by employing the Insect Life Cycle Modelling software (Version 3.0) (Azrag et al., 2017; Fand et al., 2014; Kroschel et al., 2013; Soh et al., 2018; Tonnang et al., 2013). Data collected in the life-table studies under constant temperature conditions were arranged as required by the "model builder" of ILCYM to process, analyze, and develop the phenology model that included development time and its variation, development rate, senescence, mortality, total oviposition, and relative oviposition frequency. The "validation and simulation" module of ILCYM was applied for simulating life-table parameters. The best-fit model was selected based on the Akaike Information Criterion (AIC), a well-known goodness-of-fit indicator (Akaike, 1973), or other built-in statistics (R^2, Adjusted R^2, MSE). The smaller the value of the AIC, the better is the model fit. For the selection of the best functions, statistical criteria, and biological aspects of the species were considered (Azrag et al., 2017; Sporleder et al, 2013, 2017).

2.3.2. Development time and its distribution

The cumulative probability distributions of *F. arisanus* development times under different temperatures were estimated and normalized. Frequency distributions of insect development time are usually skewed toward the longer times and it is assumed that development times of insects at different temperatures are of the same shape (Tonnang et al., 2013). The normalized development times were arranged in frequency distribution and fitted to each life stage development time in a parallel line approach, using log-development as the explanatory variable. The fitted generalized linear model to the normalized development time was the probit model for the egg-larva stage of the parasitized host and

egg-adult stage of the parasitoid, while the complementary log-log (CLL) model predicted well the development time of the puparium stage and the longevity of both males and females of the parasitoid with the mathematical expressions given as:

- Probit distribution: $F(x) = \varnothing(a_i + b l n x)$,
- CCL distribution $F(x) = 1 - \exp(-\exp(a_1 + b l n x))$.

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

2.3.3. Thermal effect on the development rate of immature stages of Fopius arisanus

The developmental rate of *F. arisanus* was computed as the inverse of developmental time (1/D), for each immature stage (egg-larva stage of the parasitized host and puparium stage of the parasitoid) and for the total developmental time from egg to adult. A simple linear regression model was fitted to *F. arisanus* stage-specific development rate [$r(T)$] using the following equation: $r(T) = a + bT$, where T is temperature, and a and b are estimates of the intercept and slope respectively. This equation was further used to estimate the lower developmental threshold, and thermal constant (K) which is the number of degree-days (DD) needed for development. The thermal constant was calculated with the formula $K = \frac{1}{b}$, where b is the slope of the linear development model described above (Campbell et al., 1974; Padmavathi et al., 2013).

Due to the inherent approximations of linear models at near-lethal temperatures, non-linear models have been used to describe developmental rate response curves over the full range of temperatures (Damos and Savopoulou-Soultani, 2008; Messenger and Flitters, 1958; Régnière, 1984; Wagner et al., 1984). Based on AIC and R2, the nonlinear model Logan type I (Logan et al., 1976) provided an excellent description of the temperature-dependent development rate of *F. arisanus* across all temperatures tested respectively for the egg-larva stage of the parasitized host, the puparium and egg-adult stages of the parasitoid. The mathematical expression of this model is provided as:

$$r(T) = Y\left(e^{(pT)} - e^{\left(pT_{max} - \frac{(T_{max}-T)}{v}\right)}\right)$$

whereby $r(T)$ refers to the development rate of the insect at temperature T, T_{max} is the maximum lethal temperature, while Y, p, and v are constants values. This model estimated the maximum temperature threshold where there is no development.

2.3.4. Immature stage mortality rate

The mortality rate was calculated from the cumulative frequency of cohort survivors. Therefore, by using AIC and R^2, a second-order exponential polynomial function was fitted to describe the relationship between the mortality rate of immature stage and temperature. The expression of the model is:

$$m(T) = e^{\left(b_1 + b_2 T + b_3 T^2\right)}$$

where m(T) is the mortality rate, b_1, b_2 and b_3 are model coefficients and T is the rearing temperature.

2.3.5. Temperature-dependent senescence and fecundity

Senescence is defined as a decline in fitness traits due to aging, but in practice, senescence is usually assessed through simple demographic variables such as longevity and fecundity (Azrag et al., 2017; Boggs, 2009). The ILCYM software uses this parameter rather than mortality to differentiate it from immature stage mortality (Tonnang et al., 2013). In our study, the mean survival time of adults was determined for both sexes and the inverse of the male and female life span was plotted against temperature. The following exponential simple function was fitted to express the temperature dependence of adult senescence (Tonnang et al., 2013):

$$s(T) = b_1 \exp(b_2 T)$$

where s (T) is the adult senescence rate and b_1 and b_2 are model coefficients.

A second-order exponential polynomial function was fitted to describe the relationship between temperature and the total number of eggs laid per female (Azrag et al., 2017; Soh et al., 2018). The following equation of the model was used:

$$m(T) = e^{\left(b_1 + b_2 T + b_3 T^2\right)}$$

where m(T) is the mortality rate, b_1, b_2 and b_3 are model coefficients and T is the rearing temperature.

2.4. Model validation

The validation module included in ILCYM software allowed evaluation of the phenology model's ability to reproduce the species behavior under variable temperature conditions. This was done by comparing experimental life table data obtained from variable temperature studies in a screenhouse with model initial outputs. Validation of the established model was performed using stochastic simulations and daily minimum and maximum temperatures collected from 2014 at the IITA-Cameroon campus were used.

2.5. Life table parameters at four contrasting agro-ecological zones of Cameroon

The models developed for *F. arisanus* demographic parameters were used to estimate its life table parameters, including net reproduction rate (R_0), mean generation time (T), intrinsic rate of natural increase (r_m), finite rate of increase (λ), and doubling time (D_t). Stochastic simulations were performed for one (1) year period at variable temperatures in four contrasting agro-ecological zones of Cameroon using the simulation module in ILCYM. The simulations are intended to show how temperature can potentially affect *F. arisanus* population growth in each agro-ecological zone where *B. dorsalis* is a major pest of fruit trees. These agro-ecological zones, delimited by the Institute of Agricultural Research for Development (IRAD) (Ngom et al., 2014), were: 1) High Guinea Savannah (HGS) (Garoua: N 09.340°, E 13.5280°, 221 masl, with a mean temperature of 29.7 °C); 2) Western Highlands with mono-modal rainfall (WH-MR) (Bambui: N 06.4228°, E 10.21923°, 1232 masl, with a mean temperature of 22.6 °C); 3) Humid Forest with mono-modal rainfall (HR-MR) (Njombe: N 04.58464°, E 9.64392°, 149 masl, with a mean temperature of 28.3 °C) and 4) Humid Forest with bimodal rainfall (HF-BR) (Mbalmayo: N 03.46795°, E 011.48284°; 663 masl, with a mean temperature of 25.0 °C). Minimum and maximum temperatures collected in 2016 in Garoua, Bambui, Njombe, and Mblamyo with HOBO Pro v2 Temp/RH were used to simulate life table parameters in each agro-ecological zone.

2.6. Additional analyses

Generalized Linear Models (GLMs) with binomial error were used to test the effects of constant temperatures on pupal recovery (proportions of developed puparia), empty puparia, sex-ratio, and adult emergence. In the case of over-dispersion of data, a GLM with a quasi-binomial distribution error was used. Data on development time, longevity, APOP, TPOP, oviposition period being duration data, a GLM with Gamma error (log link) was used, while the GLM with Gaussian error was used for fecundity and life table parameters. Tukey's HSD was used in pair-wise comparison of means. All analyses were performed with R

version 3.6.2 (R Development Core Team, 2019).

3. Results

3.1. Development time models and values

Fopius arisanus completed its development from egg to adult at all the temperatures tested, except at 35 °C (Table 1). The variability in the development times was best described by the logit and complementary log-log models respectively for the egg-larva stage of the parasitized host ($R^2 = 0.95$, AIC = 462.4) and puparium stage of the parasitoid ($R^2 = 0.99$, AIC = 476.2) (Table 2). Estimated mean development time required for the egg-larva stage of the parasitized host decreased with increasing temperature (Table 1). A similar trend was observed for the puparium stage of the parasitoid (Table 1). Development time from egg to adult was longest at 15 °C (64.9 ± 0.37 days) and shortest at 28 (19.9 ± 11 days) and 30 °C (19.9 ± 12 days) (Table 1).

Longevity of both adult female and male *F. arisanus* was well described by the complementary log-log model ($R^2 = 0.95$–0.96, AIC = 831.2–1089; Table 2), with females and males living longest at 15 °C and shortest at 30 °C (Table 1).

3.2. Development rate

The relationship between the developmental rate and temperature was described by the linear regression and Logan type I models for all immature stages and from egg to adult (Fig. 2; Table 3).

The thermal constant (K) of *F. arisanus* increased with age: the egg-larva stage of the parasitized host required 175.4 degree-days, while the puparium stage of the parasitoid needed 222.2 degree-days (Table 3). Degree-days needed for development from egg to adult were 403.6 degree-days. The lower thermal development thresholds (T_{min}) estimated by the linear regressions were 8.00 for the egg-larva stage of the parasitized host and 7.81 °C for the puparium stage of the parasitoid, whereas the maximum development thresholds (T_{max}) estimated by the Logan type I model were similar (Table 3). T_{min} and T_{max} for development from egg to adult were estimated respectively at 8.15 and 34.2 °C (Table 3).

3.3. Mortality of immature stages and adult senescence

The effect of temperature on the mortality of *F. arisanus* immature life stages was well described by a second-order polynomial function for

Table 1

Mean development time of immature life stages (days) and adult survival (days) estimated by probit (egg-larva stage of the parasitized host) and complementary log-log distributions models for *Fopius arisanus* reared at six constant temperatures.

Temperature (°C)	Development time (days)			Adult longevity (days)	
	Egg-larva[a]	Pupa[b]	Egg to adult	Female	Male
15	28.7 ± 0.27a	33.6 ± 0.40a	64.9 ± 0.37a	19.6 ± 2.14a	27.7 ± 2.24a
20	14.1 ± 0.12b	18.9 ± 0.24b	34.3 ± 0.19b	20.0 ± 2.16a	16.4 ± 1.71a
25	9.45 ± 0.09c	11.3 ± 0.14c	21.6 ± 0.13c	17.9 ± 1.56a	21.2 ± 1.78a
28	8.37 ± 0.07d	10.9 ± 0.15c	19.9 ± 0.11c	5.66 ± 0.71b	3.03 ± 0.37b
30	8.74 ± 0.07dc	10.8 ± 0.15c	19.9 ± 0.12c	1.55 ± 0.19c	1.30 ± 0.13c
35[3]	–	–	–	–	–

Means in the same column followed by the same letter are not significantly different (Tukey HSD test, $P > 0.05$).
[a] Egg-larva stage of the parasitized host.
[b] Puparium stage of the parasitoid;[3]No development occurred.

Table 2

Estimated model parameters of the cumulative distribution functions fitted to normalized development time frequencies for immature life stages and adult survival of *F. arisanus*.

Temperature (°C)	Developmental stages			Adult longevity	
	Egg-larva[a]	Puparium[b]	Egg to adult	Female	Male
Intercept (a)					
15	−34.95 ± 0.848	−29.99 ± 0.577	−124.6 ± 2.76	−3.7 ± 0.063	−4.036 ± 0.08
20	−27.55 ± 0.676	−25.14 ± 0.482	−105.6 ± 2.341	−3.728 ± 0.063	−3.46 ± 0.072
25	−23.37 ± 0.571	−20.78 ± 0.402	−91.76 ± 2.036	−3.597 ± 0.059	−3.739 ± 0.074
28	−22.12 ± 0.540	−20.53 ± 0.397	−89.33 ± 1.983	−2.31 ± 0.046	−1.593 ± 0.051
30	−22.57 ± 0.555	−20.44 ± 0.396	−89.37 ± 1.984	−0.857 ± 0.049	−0.652 ± 0.054
35[c]	–	–	–	–	–
Slope (b)	10.4 ± 0.25	8.43 ± 0.16	29.9 ± 0.66	1.12 ± 0.02	1.11 ± 0.02
R^2	0.95	0.99	0.98	0.96	0.95
AIC	462.4	476.2	469.9	1089	831.2

[a] Egg-larva stage of the parasitized host.
[b] Puparium stage of the parasitoid.
[c] No development occurred; AIC: Akaike Information Criterion.

all the immature stages (Table 4 and Fig. 3). This mortality was significantly influenced by temperature for both immature stages (egg-larva stage of the parasitized host: $P < 0.001$; puparium stage of the parasitoid: $P < 0.044$; Table 4) and ranged from 34.4 to 100% and 2–100% for the egg-larva stage of the parasitized host and puparium stage of the parasitoid respectively. Least and highest mortality of the egg-larva stage of the parasitized host occurred respectively at 20 °C (34.4%) and 35 °C (100%) (Fig. 3). Pupa mortality showed a similar temperature response, but the mortality rates were lower than reported for the egg-larva stage of the parasitized host within the range of 20–28 °C (Fig. 3).

The ILCYM software uses senescence instead of adult mortality and the simple exponential functions produced the best fit of adult senescence in response to the temperatures used in our study (Females: AIC = −12.8, $R^2 = 0.97$; Males: AIC = −14.0, $R^2 = 0.99$; Table 4; Fig. 4). Both female ($P < 0.002$) and male ($P < 0.001$) senescence were significantly affected by the temperature (Table 4).

3.4. Adult reproduction and emergence

Because *F. arisanus* did not oviposit at 30 °C, only the results from 15, 20, 25, and 28 °C were used in the analyses. Pre-oviposition period (APOP), total pre-oviposition period (TPOP), reproductive periods and fecundities were significantly affected by temperature regime (APOP: F = 14.7; df = 3, 12; $P < 0.001$; TPOP: F = 85.5; df = 3, 12; $P < 0.001$; reproductive periods: F = 16.4; df = 3, 12; $P < 0.001$; $P < 0.001$; fecundity: $F_{3, 12} = 28.0$; df = 3, 12; $P < 0.001$; $P < 0.001$; Table 5). At 15 °C, female reproduction did not start until ≈24 days after emergence, which was much later than those maintained at constant temperatures of 20, 25, and 28 °C. The mean oviposition period was longest at intermediate constant temperatures of 20 and 25 °C and shortest at both extreme temperatures (Table 5). The mean number of eggs per female ranged from 9.02 to 167.6 eggs, with the highest reproduction value at 20 °C and the lowest at 28 °C. The second-degree polynomial function described well the response of the parasitoid's fecundity to temperature (Table 4; Fig. 5), with a significant effect on female oviposition ($P < 0.001$). The function estimated the optimum temperature for reproduction at 22 °C, with 251 eggs/female, within the temperature range of 20–25 °C (Fig. 5).

Pupal recovery (proportions of developed puparia) and adult emergence differed significantly among temperatures (pupal recovery: $F_{4, 15} = 3.73$; $P < 0.027$; adult emergence: $F_{4, 15} = 4.89$; $P < 0.010$; Table 6).
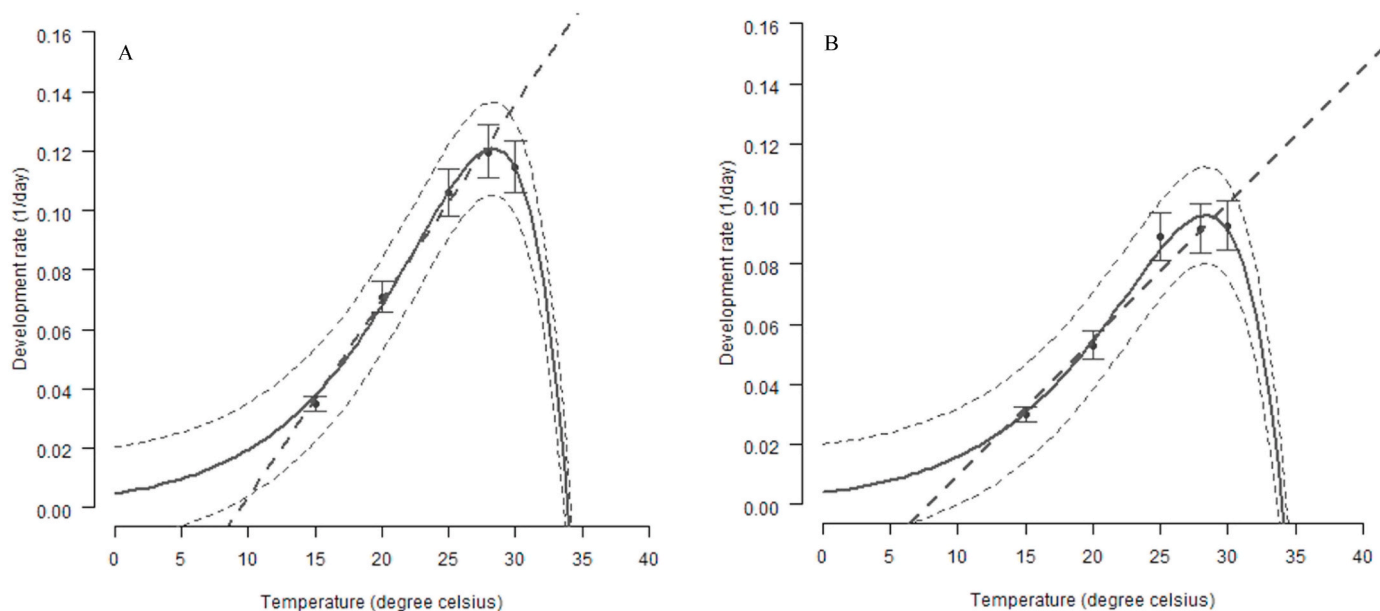
Fig. 2. Temperature-dependent developmental rate of *Fopius arisanus*: A) egg-larva stage of the parasitized host; B) puparium stage of the parasitoid. The points and bars represent the observed values and standard deviation of the mean respectively. Fitted models are the straight line for linear regression and solid curved line for the Logan type I model. Dashed lines above and below represent the upper and lower 95% confidence bands.

Table 3
Estimated parameters of the linear regressions and Logan type I model tted to median development rate (1/d) for immature life stages of *F. arisanus*.

Parameters	Developmental stage		
	Egg-larva[a]	Puparium[b]	Egg to adult
Linear regression			
a	−0.046	−0.035	−0.020
b	0.006	0.005	0.002
K (DD)	175.4	222.2	403.6
T_{min} (°C)	8.00	7.81	8.15
Logan type I			
T_{max} (°C)	34.0 ± 0.004	34.0 ± 0.003	34.2 ± 0.003
γ	0.010 ± 0.002	0.009 ± 0.002	0.004 ± 0.001
ρ	0.170 ± 2.071	0.169 ± 2.563	0.167 ± 1.443
ν	5.283 ± 0.035	5.407 ± 0.037	5.358 ± 0.024
R^2	0.97	0.94	0.98
AIC	−21.3	−21.0	−33.7

[a] Egg-larva stage of the parasitized host.
[b] Puparium stage of the parasitoid; T_{min}: lower developmental threshold; T_{max}: maximum lethal temperature; a: intercept; b: slope; γ, ρ, ν are constants values; AIC: Akaike Information Criterion.

Table 4
Estimated parameters of the second-degree polynomial (mortality and reproduction) and exponential simple (senescence) functions fitted to immature stage mortality rate, adult senescence rate and fecundity of *Fopius arisanus*.

Model parameters	Mortality		Senescence		Fecundity
	Egg-larva[a]	Puparium[b]	Female	Male	
b1	3.431 ± 0.000	2.577 ± 0.004	0.000 ± 0.000	0.000 ± 0.000	−41.18 ± 0.001
b2	−0.386 ± 0.005	−0.471 ± 0.053	0.530 ± 0.000	0.450 ± 0.000	4.216 ± 0.012
b3	0.008 ± 0.000	0.011 ± 0.002	–	–	−0.095 ± 0.001
F	161.0	22.0	112.2	221.5	392.1
P	0.001	0.016	0.002	0.001	0.001
R^2	0.99	0.94	0.97	0.99	0.99
AIC	−20.9	−4.39	−12.8	−14.0	41.7

[a] Egg-larva stage of the parasitized host.
[b] Puparium stage of the parasitoid; b_1, b_2, and b_3 are model coefficients; AIC: Akaike Information Criterion.

The highest pupal recovery occurred at 25 °C (49.3 ± 5.23%) and the lowest at 15 °C (23.2 ± 7.78%) (Table 6). Similarly, the highest adult emergence was obtained at 20 °C (64.7 ± 4.76%) and the lowest at 30 °C (22.7 ± 7.56) (Table 6). The relative frequency of empty puparia recovery was not affected by temperature ($F_{4, 15}$ = 0.94; P = 0.466) and ranged from 2.2 to 8.21%. Sex ratio was female biased but was not affected by temperatures ($F_{4, 15}$ = 0.68; P = 0.614).

3.5. Validation of the model

Phenology model validation of *F. arisanus* was carried under variable temperatures at 15.1–36.6 °C, with an average temperature of 24.3 °C. **The** gross reproductive rate was the only population parameter that was well predicted when compared with observed data, a significant difference was obtained for development time, mortality, net reproductive rate, intrinsic rate of increase, finite rate of increase, mean generation time, and doubling time (Table 7).

3.6. Population parameters

Stochastic simulation under variable temperatures within 1 year showed that the bimodal rainfall humid forest (BRHF) (Mbalmayo) presents better thermal conditions for *F. arisanus* population growth, followed by the Western Highlands (Bambui) (Table 8). In this suitable agro-ecological zone, the gross reproductive rate (GRR) and the net reproductive rate (R_0) were 53.2 and 4.24 eggs/generation respectively and the intrinsic rate of natural increase (r_m) reached a value of 0.054. Moreover, *F. arisanus* populations potentially might increase with a finite rate of about 1.06, while population double in 13 days. Furthermore, the parasitoid would take about 26.9 days to complete one generation. According to mean generation time (T), 2, 6, 11, and 14 generations of *F. arisanus* might develop yearly in HGS (Garoua), HR-MR (Njombe), WH-MR (Bambui), and HR-BR (Mblamayo) respectively.
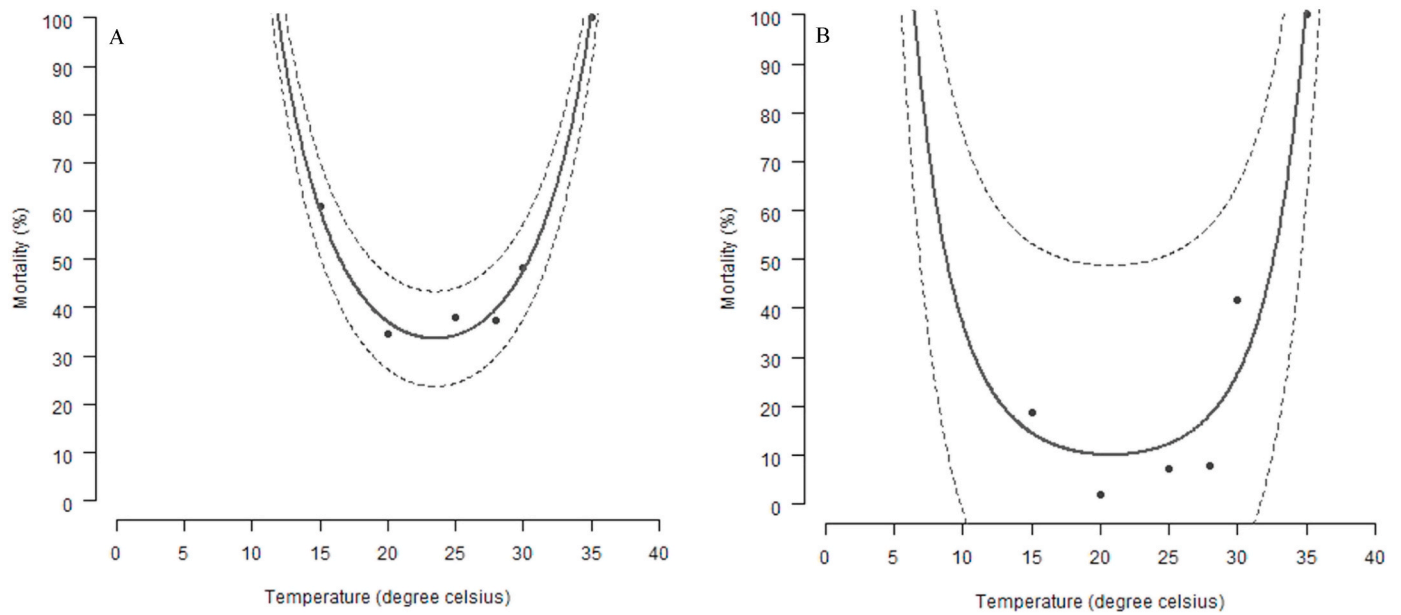
Fig. 3. Temperature-dependent mortality rate of *Fopius arisanus*: A) egg-larva stage of the parasitized host; B) puparium stage of the parasitoid. The points and bars represent the observed values and standard deviation of the mean respectively. Fitted models are the straight line for linear regression and solid curved line for the second-degree polynomial model. Dashed lines above and below represent the upper and lower 95% confidence bands.
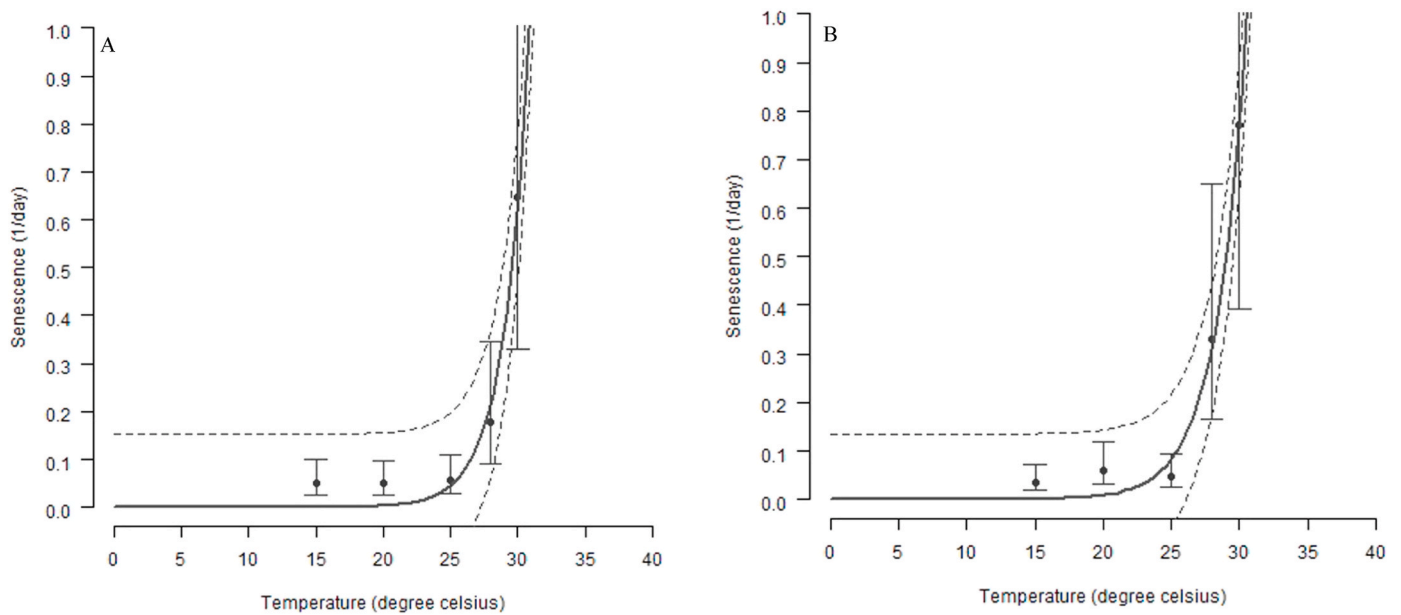

Fig. 4. Temperature-dependent senescence rate of *Fopius arisanus*: A) egg-larva stage of the parasitized host; B) puparium stage of the parasitoid. The points and bars represent the observed values and standard deviation of the mean respectively. Fitted models are the straight line for linear regression and solid curved line for the exponential simple functions. Dashed lines above and below represent the upper and lower 95% confidence bands.

4. 4. discussion

4.1. 4.1 thermal biology of Fopius arisanus

This study provides the first complete information – including development, survival, reproduction, and sex-ratio – on the effect of a broad range of temperatures on the demography of *F. arisanus*, one of the most important parasitoids of *Bactrocera* species (Mohamed et al., 2010; Rousse et al., 2005). It also reports for the first time results of a full demographic analysis of *F. arisanus* on *B. dorsalis* using a phenology model through an algorithm used in ILCYM which has been applied in numerous similar studies (Azrag et al., 2017; Khadioli et al., 2014;

Mujica et al., 2017; Soh et al., 2018; Tanga et al., 2018).

Fopius arisanus completed development between 15 and 30 °C but not at 35 °C. The values obtained from the model developed for the whole development from egg to adult are close to those reported by Appiah et al. (2013) with *B. invadens* (= *B. dorsalis*) as host. The complementary log-log distribution demonstrated that female and male *F. arisanus* exposed to temperatures of 15 and 20 °C survived longer as reported by Appiah et al. (2013) at similar conditions. These authors reported female and male longevities of 131 and 110 days at 15 °C, 127.7 and 106.3 days at 20 °C, compared with 20.03 and 28.39 days at 15 °C, 20.6 and 17.1 days at 20 °C in the present study. A key difference between our study and that of Appiah et al. (2013) is likely to be related

Table 5

Means (±SE) of the adult pre-oviposition period (APOP), total pre-oviposition period of females counted from birth (TPOP), oviposition period and fecundity of *Fopius arisanus* reared on *Bactrocera dorsalis* under five constant temperatures.

Temperature (°C)	APOP (d)	TPOP (d)	Oviposition period (d)	Fecundity (eggs/femelle)
15	23.6 ± 3.80a	86.9 ± 4.16a	7.19 ± 2.17b	12.38 ± 7.053c
20	7.51 ± 0.34c	41.6 ± 0.68b	22.4 ± 3.05a	163.6 ± 19.83a
25	12.8 ± 2.80b	35.1 ± 3.32c	17.7 ± 0.30a	108.5 ± 19.27b
28	7.81 ± 0.61c	27.8 ± 0.83d	7.08 ± 0.57b	9.019 ± 2.304c
30[a]	–	–	–	–

Means in the same column followed by the same letter are not significantly different (Tukey HSD test, $P < 0.05$).
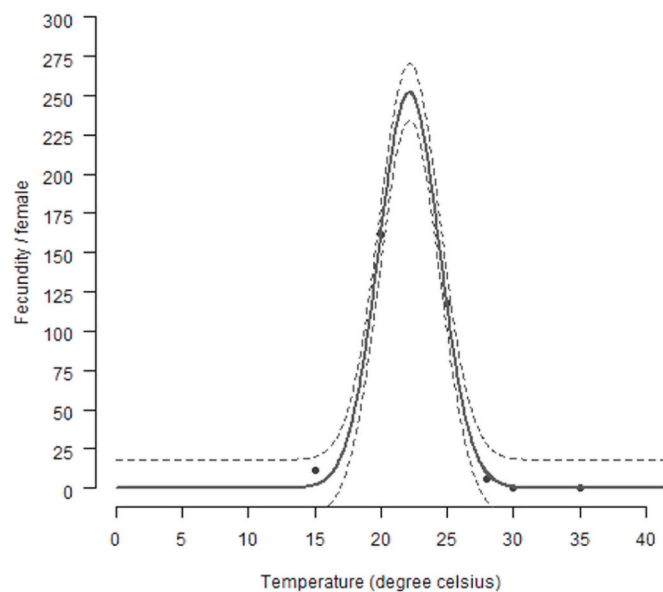
[a] No reproduction occurred.

Fig. 5. Temperature-dependent fecundity of *Fopius arisanus*. The points and bars represent the observed values and standard deviation of the mean respectively. Fitted models are the straight line for linear regression and solid curved line for the second-degree polynomial model. Dashed lines above and below represent the upper and lower 95% confidence bands.

Table 6

Mean (±SE) percentage of recovered pupae of *Fopius arisanus* and *Bactrocera dorsalis*, *F. arisanus* adult emergence and *F. arisanus* sex ratio at five constant temperatures.

Temperature (°C)	Pupal recovery (%)	Adult emergence (%)	Empty pupae (%)	Sex ratio[a]
15	23.2 ± 7.78b	34.1 ± 4.15bc	8.21 ± 4.56a	0.69 ± 0.07a
20	40.4 ± 7.14a	64.7 ± 4.76a	2.87 ± 1.20a	0.62 ± 0.10a
25	49.3 ± 5.23a	46.7 ± 5.48 ab	2.20 ± 0.97a	0.70 ± 0.03a
28	46.45 ± 4.25a	49.4 ± 6.47 ab	4.61 ± 2.58a	0.74 ± 0.04a
30	48.1 ± 2.35a	22.7 ± 7.56c	4.01 ± 1.05a	0.81 ± 0.11a

Means in the same column followed by the same letter are not significantly different (Tukey HSD test, $P > 0.05$).

[a] Proportion of females.

Table 7

Life-table statistic summary from simulated and observed life-table parameters, development time, and mortality of *Fopius arisanus*.

Life table parameters	Simulated	Observed	P
Intrinsic rate of natural increase (r_m)	0.039 ± 0.016	0.056	0.001
Net reproduction rate (R_0)	3.11 ± 1.31	19.0	0.001
Gross reproductive rate (GRR)	32.1 ± 26.5	37.6	**0.328**
Mean generation time (T)	28.4 ± 1.15	52.8	0.001
Finite rate of increase (λ)	1.04 ± 0.02	1.06	0.001
Doubling time (D_t)	19.8 ± 13.5	12.4	0.023
Development time (d)			
Egg-larva[a]	10.7 ± 0.26	9.86	0.001
Puparium[b]	14.1 ± 0.53	14.7	0.001
Mortality (%)			
Egg-larva[a]	0.37 ± 0.06	0.61	0.001
Puparium[b]	0.64 ± 0.10	0.43	0.001

[a] Egg-larva stage of the parasitized host.

[b] Puparium stage of the parasitoid.

to the rearing conditions of the immature stages. In contrast, *F. arisanus* female longevity at 25 °C in our study (17.9 days) is close to that reported by Harris et al. (2007) at 25 °C (18 days) and Vargas et al. (2002) at 26 ± 2 °C (17.3 days) with *B. dorsalis* as the host, and by Groth et al. (2016) at 25 ± 2 °C (25.2 days) with *C. capitata* as the host.

The lower temperature threshold of development for immature stage (egg-adult) estimated using the linear regression equation in our study is 2° C less than that reported by Appiah et al. (2013) on the same species and equal to the lower threshold for the development of the egg stage (≈8 °C) of *B. dorsalis* (the same population used to maintain *F. arisanus*) obtained by Dongmo et al. (2021). The synchrony between the lower temperature threshold of the host and its parasitoid favors an outcome of potentially significant impact on the development of the parasitoid inside its host. This may vary with seasons and is only true at lower temperatures because all life stages of *B. dorsalis* tolerate higher temperatures than those of *F. arisanus* (Dongmo et al., 2021; Vargas et al., 1996; Yang et al., 1994). For example, in cool but sunny spring, when the parasitoid *Cotesia melitaearum* (Wilkinson, 1937) emerge, most larvae of its host *Melitaea cinxia* (Linnaeus, 1758) have already pupated and are no longer available for parasitization, while in warmer springs, the synchrony between both organisms is maintained and the level of parasitization is high (Hance et al., 2007; Van der Putten et al., 2004).

Temperature also induced significant mortality of immature stages of parasitized *B. dorsalis*, being greater than 30% at all the temperature tested, which is consistent with the results of Baustista et al. (2004) who reported 38% mortality of *B. dorsalis* eggs exposed to *F. arisanus* at 22.4 °C. In addition to the thermal effect, mortality of immature stages, also known as non-reproductive mortality, may also be associated with host egg injuries caused by (1) drilling movements of parasitoid ovipositor through the chorion during oviposition, (2) introduction of toxic substances, (3) introduction of microbial pathogens into oviposition punctures, or (4) corking-off of lesions through the chorion (Bautista et al., 2004; Moretti and Calvitti, 2003). The mechanisms involved in non-reproductive mortality may also be influenced by parasitoid age, host density, host age, parasitoid species, and parasitoid host (Pizzol et al., 2012). According to Abram et al. (2016), parasitoids-induced host-egg abortion is rarely explicitly accounted for, leading to under-estimation of the ecosystem services provided by biological control agents.

At the temperature range of 20–30 °C, pupal recovery and percentage of adult emergence were high. Similar values of percentage emergence were reported at 25 °C with *F. arisanus* reared on *B. invadens* (= *B. dorsalis*) (Appiah et al., 2013) and *C. capitata* (Groth et al., 2017; Zenil et al., 2004) as hosts, as well as for other parasitoids like *Diachasmimorpha longicaudata* (Ashmead, 1905) (Meirelles et al., 2013) and *Doryctobracon brasiliensis* (Szépligeti) (Poncio et al., 2016) parasitizing larva of *Anastrepha fraterculus* (Wiedemann). Fecundity per female estimated by the second-order polynomial function was optimum at

Table 8
Life table parameters of *Fopius arisanus* simulated for four agroecological zones of Cameroon using mean daily minimum and maximum temperature data (initial egg number (n) = 100), with GRR: gross reproductive rate, R0: net reproductive rate, r: intrinsic rate of increase, λ: finite rate of increase, T: mean generation time and Dt: doubling time.

AEZ	Location	Temperatures		Life table parameters					
		T_{min}	T_{max}	r	R_o	GRR	T	λ	D_t
HGS	Garoua	23.8	35.6	-0.003 ± 0.002d	0.87 ± 0.36c	19.0 ± 10.6c	177.7 ± 1.33a	0.997 ± 0.002d	-1714 ± 105.3b
WH-MR	Bambui	17.0	27.9	0.023 ± 0.003b	2.20 ± 0.25b	26.3 ± 5.70b	32.4 ± 0.47c	1.024 ± 0.004b	33.8 ± 7.27a
HF-MR	Njombe	23.3	33.3	0.009 ± 0.001c	1.81 ± 0.10b	15.8 ± 2.73d	62.2 ± 0.20b	1.010 ± 0.001c	77.1 ± 9.67a
HF-BR	Mbalamyo	20.5	29.6	0.054 ± 0.002a	4.24 ± 0.21a	53.2 ± 5.58a	26.9 ± 0.19d	1.055 ± 0.002a	13.0 ± 0.54a
$F_{3,16}$ (P value)				104.1 (0.001)	33.3 (0.001)	6.30 (0.005)	97.3 (0.001)	121.1 (0.001)	4.27 (0.025)

T_{min}: yearly minimum temperature; T_{max}: yearly maximum temperature.
HGS: High Guinea Savannah; WH-MR: Western Highlands with mono-modal rainfall; HR-MR: Humid Forest with mono-modal rainfall; HF-BR: Humid Forest with bimodal rainfall.
Means in the same column followed by the same letter are not significantly different (Tukey HSD test, *P* > 0.05).

22 °C (≈251 eggs/female), with the temperature range of 20–25 °C being more appropriate for reproduction. With *B. dorsalis* as host, *F. arisanus* produced 134.8 ± 20.5 eggs/female at ambient temperatures of 22–24 °C (Bautista et al., 1998) and 117.4 ± 24.7 eggs/female at 26 ± 2 °C (Vargas et al., 2002). Similar values were obtained with *C. capitata* as host: 133 ± 20.5 eggs/female at 24 ± 2 °C (Argov et al., 2011) and 123.1 ± 1.16 eggs per female at 25 °C and 157.8 ± 0.8 at 26.8 ± 0.4 °C (Argov et al., 2011; Zenil et al., 2004). These values are closer to those reported in our study for 20 and 25 °C.

Validation of the phenology model of *F. arisanus* was carried out by comparing experimental life table data obtained from variable temperature studies in the screenhouse with the initial outputs modeled. The gross reproductive rate was the only population parameter that was properly predicted by the model. Although no significant difference was noted, the simulated values of the intrinsic rate of increase, finite rate of increase, and development time of immature stages were closer to that observed. However, differences noted between simulated and observed may be related to deviances observed in the model due to little data at extreme temperatures (Fand et al., 2014; Mujica et al., 2017; Régnière et al., 2012) caused by high mortality of immature stages. Therefore, we recommend that more data at extreme temperatures should be generated to increase the precision of estimated parameters.

4.2. Implications for Bactrocera dorsalis control in a changing climate

The favorable temperatures for immature development and reproduction of *F. arisanus* ranged between 20 and 30 °C, a temperature range commonly found in tropical and even sub-tropical regions of Africa (Leroux, 2001). This temperature range is also known as adequate for parasitism as observed for several fruit fly parasitoids (Appiah et al., 2013; Hurtrel et al., 2001; Poncio et al., 2016). Although the extreme temperatures of 15 and 35 °C had a detrimental effect on the development, the parasitoid can survive in the field, since extreme temperatures are rare for long periods and generally occur during the day (Groth et al., 2017; Hurtrel et al., 2001). But for reproduction, high temperatures may be less suitable because female *F. arisanus* emerging at 30 °C failed to lay eggs. This may explain why biological control using *F. arisanus* release is ineffective under certain climatic conditions. In the context of rising global temperatures, this failure could contribute to asymmetrical outcomes in host-parasitoid interaction in reducing parasitoid efficacy and its possible exclusion, but not its host, from agro-ecologies in which the two currently co-exist.

Stochastic simulation results at variable temperatures demonstrated that HF-BR (Mbalmayo) presents a suitable temperature (25 °C) for *F. arisanus* population growth. In addition to this temperature, Nanga et al. (2019) demonstrated that *F. arisanus* was able to parasitize *B. dorsalis* in different fruit species with different phenologies, mainly *Irvingia* species. These fruit species are widely spread in this zone (Kuate et al., 2006; Tchoundjeu et al., 2006), suggesting that the parasitoid could survive and establish permanently. The intrinsic rate of

population increase (r_m) is a useful index of population growth under a given set of growing conditions (Jervis et al., 2005). A population generally increases only when $R_0 > 1$ and $r_m > 0$. In the present study, $R_0 > 1$ and r > 0 in WH-MR (Bambui), HF-BR (Njombe), and HF-BR (Mbalmayo), but a significant population increase could be observed in HF-BR (Mbalmayo), suggesting that *F. arisanus* populations would eventually grow at a constant exponential rate of 0.054 per individual per day or a doubling time of 13 days. In the same agro-ecology, the finite rate of population increase showed an aggregation of more than one individual per female from one generation to another. At a constant temperature of 25 °C (mean temperature found in this zone), the intrinsic rate of increase and generation time of *B. dorsalis* were respectively 0.12 and 52 days (Dongmo et al., 2021). Based on the present simulations, the generation time of the parasitoid and its intrinsic rate of increase were considerably lower compared with those of its host *B. dorsalis* that was earlier mentioned. These results suggest the significant potential of using *F. arisanus* to control *B. dorsalis* in this agro-ecology, but the parasitoid alone is not likely to be enough to manage pest populations. Integration of biological control with other control options such as bait sprays, male annihilation, orchard sanitation, fruit bagging or wrapping and early harvesting may reduce the pest population growth and enhance the effectiveness of the parasitoid (Appiah et al., 2014; Ekesi and Billah, 2006; Hanna et al., 2008b).

5. Conclusion

The present study shows the importance of a wide range of constant and variable temperatures on the developmental rate, mortality, longevity, oviposition, and fecundity of *F. arisanus*. Our models indicate that *F. arisanus* can be used for fruit fly control in environments where temperatures fluctuate between 20 and 30 °C. Increasing temperatures under climate change scenarios may therefore favor the host pest since it will grow unchecked at temperatures above 30 °C. The temperature-driven phenology models developed in this study, when linked to geographic information system (GIS) (e.g., Kroschel et al., 2014; Tanga et al., 2018), will help to globally map, the potential distribution and abundance of *F. arisanus* where *B. dorsalis* is presently well established and to project its potential distribution where it is not present as well as it potential response to global warming. At present, the only studies available with information predicting potential favorable *F. arisanus* establishment locations rely on occurrence data (Lane et al., 2018; Müller et al., 2019). Present and future distribution models based on phenology data have become very useful tools for comparison with the existing distribution prediction models.

CRediT authorship contribution statement

Samuel Nanga Nanga: Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Writing original draft preparation, Writing – review & editing, Visualization. **S.**

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