Bulletin of Entomological Research

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Temperature-dependent development, survival and reproduction of *Apanteles hemara* (Nixon) (Hymenoptera: Braconidae) on *Spoladea recurvalis* (F.) (Lepidoptera: Crambidae)

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Research Paper

Cite this article: Agbodzavu MK, Osiemo-Lagat Z, Gikungu M, Ekesi S, Fiaboe KKM (2020). Temperature-dependent development, survival and reproduction of *Apanteles hemara* (Nixon) (Hymenoptera: Braconidae) on *Spoladea recurvalis* (F.) (Lepidoptera: Crambidae). *Bulletin of Entomological Research* **110**, 577–587. https://doi.org/10.1017/S0007485319000920

Received: 5 October 2019
Revised: 7 December 2019
Accepted: 16 December 2019
First published online: 18 February 2020

Keywords:
Amaranth; developmental thresholds; fecundity; life history; models; sex ratio

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Abstract

The temperature-dependent development of *Apanteles hemara* (Nixon), a larval endoparasitoid of the devastating amaranth pest *Spoladea recurvalis* (F.) was studied in the laboratory at six constant temperatures (10, 15, 20, 25, 30 and 35 °C), a photoperiod of 12L:12D and a relative humidity of 60–70%. Developmental time decreased significantly with increasing temperature within the range of 15–30 °C. The parasitoid's pupal mortality, successful parasitism rate, adult emergence rate and longevity, sex ratio and fecundity were affected by temperature. The population of *A. hemara* failed to develop at 10 and 35 °C. The development threshold (T_{min}) and the thermal constant (K) were calculated by the linear model while the lethal temperature (T_{max}) was determined by the Lactin-1 model. The estimated values of T_{min}, T_{max} and K by the two models were 10.3 °C, 35.0 °C and 185.18 DD respectively for the total immature development. The estimated value of the optimum temperature using the Taylor model was 30.8 °C. This is the first study to report on the effect of temperature on the developmental parameters of *A. hemara* giving an insight into its biology. The implications of these findings for the use of *A. hemara* in biological control are discussed.

Introduction

Amaranth is a plant with a high nutritional value, whose nutrients are concentrated in leaves and grains (Santiago *et al.*, 2014). It is used in human and animal products as well as forage, silage and green manure. It has potential industrial uses in cosmetology and biodegradable plastics (Paredes-López, 2018). Amaranth is, however, attacked by a complex of lepidopteran species among which *Spoladea recurvalis* (F.) (Lepidoptera: Crambidae) is the most devastating (Chang and Ramasamy, 2016; Othim *et al.*, 2017; Agbodzavu *et al.*, unpublished data). Up to 100% yield losses due to *S. recurvalis* were reported by Kahuthia-Gathu (2011). The larvae wrap and roll amaranth leaves into shelters from which they feed skeletonizing the foliage and leaving frass on leaves often leading to entire foliage loss (Bhattacherjee and Ramdas Menon, 1964; Pande, 1972; James *et al.*, 2010). Chemical control with the use of pyrethroid is inefficient (Clarke-Harris and Fleischer, 2003) and spinosad application gave only relatively low protection against the lepidopteran complex that feeds on amaranth (Clarke-Harris *et al.*, 2004). In addition to their inefficiency, the use of insecticides is considered as non-environment friendly and costly for small-scale farmers. In a study carried by Macharia (2015) in Kenya, it was reported an increase of pesticide-related acute illness by over 70%. Therefore, the economic value of pesticide-related health cost is non-negligible (Maumbe and Swinton, 2003; Houndekon *et al.*, 2006) and is creating negative consumer sentiment around the use of insecticides which puts pressure on growers to use alternative control measures, such as biological control (Wohlfarter and Addison, 2014).

Biological control programs, whether using the introduction, conservation or augmentation approaches, are facilitated when the climatic responses of biocontrol agents are known, especially temperature (Roy *et al.*, 2002). Poor ecological adaptability of a parasitoid to the environment in the field is reported to be one of the factors explaining the failure of biological programs. Stiling (1993) meta-analyses on natural enemy failures, estimated that ~35% of biocontrol introductions or programs might have been unsuccessful because of climate-related factors (Hoddle *et al.*, 2014). Failure of *Trichogramma chilonis* (Ishii) (Hymenoptera: Trichogrammatidae) in controlling *Chilo infuscatellus* (Snellen) (Lepidoptera: Crambidae) in Uttar Pradesh, India, was due to the high temperature and low humidity prevailing during April–July (Tiwari and Tanwar, 2001) whereas in Punjab, India, it was effective in suppressing

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Chilo auricilius (Dudgeon) (Lepidoptera: Crambidae) on sugarcane by reducing its incidence from 61 to 12.6% through inundative releases (Varma *et al*., 1991). In Thailand, *Quadrastichus citrella* (Reina and La Salle) (Hymenoptera: Eulophidae) is considered one of the key factors in regulating *Phyllocnistis citrella* (Stainton) (Lepidoptera: Gracillariidae) field populations (Kernasa *et al*., 2008) and also in Israel where up to 84% parasitization of the leafminer's larvae was recorded (Argov and Rossler, 1996). However, in a study carried out by Llacer *et al*. (2006), it was reported that overwintering of *Q. citrella* in Spain may present a barrier, especially in areas where average winter temperatures are around 11 °C and could account for the low recovery rates observed on the citrus leafminer *P. citrella*. It is thus important to establish how a parasitoid will respond to a range of temperatures to predict its survival, establishment and performance in a given area as well as identify the best timing of releases.

Apanteles hemara (Nixon) (Hymenoptera: Braconidae) is a solitary koinobiont endoparasitoid reported in Africa and Asia, but detailed information on its biology is scarce. The only available literature is just based on reports of its presence in different regions. In Cape Verde Islands, the parasitoid was recovered from its host *S. recurvalis* on *Achyranthes aspera* L. (Amaranthaceae) (Papp, 1996). It was also cited in India, where the field parasitism rate reached 11% on the same host (Peter and Balasubramanian, 1984) and Iran, Qazvin province (Ghahari *et al*., 2012). Work done by Othim *et al*. (2017) showed high parasitism rates of the parasitoid in laboratory conditions. Agbodzavu *et al*. (unpublished data) found that *A. hemara* represented the most commonly found parasitoid attacking *S. recurvalis* in the field. It is, therefore, a good potential candidate for an augmentative or classical biological control for other areas where *S. recurvalis* represents a serious threat to vegetable production such as aubergines, bean, beetroot and cucurbits (James *et al*., 2010). The objective of this research was to assess the effect of temperature on the development and performance of the parasitoid *A. hemara* on its preferred host *S. recurvalis*.

Materials and methods

Rearing of Spoladea recurvalis *and* Apanteles hemara

The insects used in this experiment were reared at the insectaries of the International Centre of Insect Physiology and Ecology in Nairobi. Larvae of *S. recurvalis* were collected from a field survey of amaranth lepidopteran pests in Narok county, Transmara (0° 35′ 32.892″ N, 3° 0′ 49.14″ E) and Yatta, Machakos County (01° 08.295′ S, 037° 25.892′ E) in May and June 2014. A colony of *A. hemara* was established from pupal samples collected during a survey conducted in Yatta, Machakos County (01° 07.878′ S, 037° 33.274′ E) in June 2014. Field insects' materials were later collected from Yatta to infuse the laboratory colonies. Both *S. recurvalis* and *A. hemara* were reared according to the methods described by Othim *et al*. (2017).

Effect of different constant temperatures on the developmental time of Apanteles hemara

Newly emerged adults of *A. hemara* were isolated from the stock culture in separate cages (20 cm × 20 cm × 25 cm) and allowed to mate for 2 to 3 days. The cages were made up of Perspex materials with fine netting materials (150 µm × 150 µm mesh) fitted on the backside to allow efficient air circulation inside the cages. A sex ratio of one male to two females was used. They were fed with a drop of honey smeared on paper and hung with masking tape on one inner face of the cage and also with 10% of honey solution soaked in cotton and kept in an opened Petri dish (90 mm × 12 mm).

A single 2 to 3 days old mated naïve female wasp (with no oviposition experience) was introduced in a cage as indicated above. The cage contained 20 larvae (3–4 days old on their second instar) of *S. recurvalis* kept in an opened Petri dish for parasitization. Parasitization was observed visually. One female parasitoid was allowed to parasitized ten host larvae out of the 20; it was after that replaced by another female supplied with another batch of 20 larvae. Once the female parasitoid was observed introducing its ovipositor in a host, this host larva was removed using a fine camel brush, isolated in a vial (20 ml) plugged with cotton wool, and introduced in the incubator (Environmental chambers, SANYO MIR-553 and MIR-554, Sanyo Electrical Ltd., Tokyo, Japan), with known temperatures (i.e., 10, 15, 20, 25, 30 and 35 °C) under a relative humidity ranging from 60–70%. To maintain this range of relative humidity, two plastic boxes containing water were placed on the lower shelf of the incubator and refilled as needed. Every 2 days, fresh amaranth leaves were provided to the larvae until parasitoid cocoon formation, host pupation and subsequent emergence of parasitoid or host adults or death of larvae. A total of 200 exposed larvae for parasitization were used for each temperature. For those with effective parasitization, the developmental time of each stage of the parasitoid, the number of cocoons formed (which is termed successful parasitism rate or successful oviposition), the number of cocoons from which adult wasps emerged, the sex ratio of the emerged adults and the parasitoid pupal mortality were determined. Due to the deteriorated nature of the dead exposed host larvae, it was not possible to dissect them and assess the parasitoid egg-larval mortality.

Longevity of adults

Before adult emergence, a drop of honey was put on the internal wall of the vial to allow them to start feeding once they emerged from the cocoons. Vials were kept in an incubator set at the same conditions as mentioned above. They were followed daily at the same time. Mortality was recorded until all adult parasitoids died.

Fecundity

Due to host larvae limitations (difficulties of having continuous and sustainable colonies in laboratory conditions), fecundity was studied only at 20 and 25 °C. Newly emerged females were coupled with males of the same age in individual containers (12 cm in diameter, 6.5 cm in height) which had their top covered in the middle with fine mesh for ventilation. A drop of honey was put on the wall of the container to allow the adults to feed. Each couple was provided with 20 *S. recurvalis* larvae (3–4 days old) daily until the female died. The number of larvae offered daily was based on results of Othim *et al*. (2017), who found that the highest number of cocoon of *A. hemara* recovered after 24 h exposure on 50 larvae was 14. A fresh amaranth leaf was hung on the top of the container as a food source for the exposed larvae. A new container was used for daily exposure of the larvae. A total of 10 and 15 pairs (replicates) of wasps were used for 20 and 25 °C respectively. Daily exposed larvae were isolated individually in vials plugged with cotton wool and reared on amaranth leaves until the emergence of either a parasitoid or a moth as described above. The parasitoid lifespan was recorded as well as the pre-oviposition period, oviposition period and a post-oviposition period.

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The post-oviposition period refers to the time when a parasitoid ceased to parasitize hosts until the death of the parasitoid. Two fecundity parameters were calculated, realized fecundity as the number of parasitized larvae that developed in a cocoon (whether it developed into an adult parasitoid or not) over the life-span of the parasitoid, and fertility as the number of adult parasitoids that emerged from cocoons (Murillo *et al.*, 2012).

Data analyses

Data were subjected to Shapiro–Wilk and Bartlett tests to test for normality and homogeneity of variance respectively. The developmental durations for each life stage and adult longevity were compared between temperatures with a Dunnett test using *dunn.test* package and between sex with a Wilcoxon test because data were not normally distributed. Where data were normally distributed between sex (adult longevity), an independent samples *t* test was used. Larval and pupal mortality, as well as the parasitism rate and the emergence rate of the parasitoid, were compared between temperatures with a proportion test. The sex ratio was examined at each temperature using a χ^2 test.

The development rate was calculated as the inverse median development time (development rate = 1/median development time) (Régnière, 1984), for each immature stage (egg-larval and pupal) and plotted against temperature. The degree-day model states that the relationship between development rate $r(T)$ (1/development time in days) vs. temperature can be described by a linear equation: $r(T) = a + bT$, where T is the rearing temperature, a is the intercept and b is the slope of the linear function. The lower threshold temperature T_{min} ($T_{min} = -a/b$) and the thermal constant K (i.e., the number of degree-days above the lower threshold required to complete development, DD) ($K = 1/b$) were calculated based on the linear equation (Mathieu *et al.*, 2014). The data points for extreme temperatures (nonlinear points) were excluded. Linear functions cannot correctly capture the development rate at extreme temperatures. For that reason, three non-linear models, Taylor, Lactin-1 and Ratkowsky were used to describe the relationship between temperature and development rates. Taylor function is defined as follows $rT = R_m \times \exp(-1/2 \times ((T-T_m)/T_o)^2)$, where rT is the development rate, T the temperature, R_m the maximum development rate, T_m the optimum temperature and T_o the rate at which development rate falls away from T_m (Taylor, 1981). The Lactin-1 model is defined as $rT = \exp(aa \times T) - \exp(aa \times T_{max} - (T_{max} - T)/\Delta T)$ where rT is the development rate, T the temperature and aa, T_{max} and ΔT fitted parameters. The Ratkowsky model is formulated as $rT = (cc \times (T - T_1) \times (1 - \exp(k \times (T - T_2))))^2$ where rT is the development rate, T the temperature, T_1 and T_2 the minimum and maximum temperatures at which the rate of growth is zero, cc the slope of the regression and k a constant (Ratkowsky_83: Ratkowsky Equation Of Development Rate. Retrieved from https://rdrr.io/cran/devRate/man/ratkowsky_83.html). The *devRate* package for R (Rebaudo *et al.*, 2017) was used to quantify the relationship between development rate and temperature. All statistical analyses were done in R statistical software version 3.4.1 (R Core Team, 2017).

Results

Developmental time of Apanteles hemara at different temperatures

A. hemara larvae reared at constant 10 and 35 °C failed to complete development and died before emergence from the host, thus these data were only analysed from individuals that successfully emerged from *S. recurvalis*. At 15 °C, the egg-larval developmental time of male parasitoids was not statistically different from females ($W = 11.5$, df = 1, $P = 0.794$). The same trend was observed at 20 °C ($W = 435.5$, df = 1, $P = 0.059$) and 30 °C ($W = 744$, df = 1, $P = 0.786$). It was, however, significantly different at 25 °C ($W = 619$, df = 1, $P = 0.024$). The pupal developmental time was not significantly different between sex at 15 °C ($t = 0.099$, df = 7, $P = 0.924$) and 30 °C ($W = 827$, df = 1, $P = 0.385$). The difference was, however, significant at 20 °C ($W = 952.5$, df = 1, $P < 0.0001$) as well as at 25 °C ($W = 763.5$, df = 1, $P < 0.0001$). The total developmental time was not significantly different between males and females at 15 °C ($t = 0.355$, df = 4.35, $P = 0.739$) and at 30 °C ($W = 812$, df = 1, $P = 0.476$) but was significantly different at 20 °C ($W = 1003.5$, df = 1, $P < 0.0001$) and 25 °C ($W = 811.5$, df = 1, $P < 0.0001$) (Table 1).

The developmental time varied greatly among tested temperatures. For the males ($\chi^2 = 115.39$, df = 3, $P < 0.0001$) and females ($\chi^2 = 86.783$, df = 3, $P < 0.0001$), egg-larval developmental times were significantly different between temperatures. Similarly, there was a highly significant decrease in *A. hemara*'s pupal developmental time with increasing temperature in males ($\chi^2 = 106.32$, df = 3, $P < 0.0001$) and females ($\chi^2 = 82.509$, df = 3, $P < 0.0001$). The total developmental time was also significantly affected by the temperatures in males ($\chi^2 = 116.47$, df = 3, $P < 0.0001$) and females ($\chi^2 = 116.47$, df = 3, $P < 0.0001$) (Table 1).

Development time models and estimated values

Figures 1–3 represent estimation of linear regression, Taylor, Lactin-1 and Ratkowsky models for different stages of development. Table 2 shows the effect of temperature on the development rate of *A. hemara*.

The fit of all tested non-linear models for the dependence of development rates of *A. hemara* on temperature was significant for egg-larval and total developmental time. For egg-larval development, $F = 25.33$ and $P < 0.0001$ for the Taylor model, $F = 6.57$ and $P = 0.010$ for Ratkowsky and $F = 229.5$ and $P < 0.0001$ for Lactin-1. For total developmental time, $F = 55.24$ and $P < 0.0001$ for the Taylor model, $F = 22.62$ and $P < 0.0001$ for Ratkowsky and $F = 602.8$ and $P < 0.0001$ for Lactin-1. For the pupal development time, only Lactin-1 fit was significant ($F = 118.1$, $P < 0.0001$). Base on R^2, Lactin-1 was retained as it best fits the data for larval, pupal and total development rates (Table 2). The Lactin-1 model estimated the upper threshold temperature for development at 35.0 °C for larval, pupal and total development stages. Since, the Lactin-1 model does not estimate the optimum temperature, it was derived from the Taylor-81 model and was estimated at 30.8 °C for the total development stage.

Using the linear model, the lower temperature (T_{min}) and the sum of effective temperatures (K) for development were 10.1 °C and 106.38 DD for the egg-larval stage. They were 10.1 °C and 75.76 DD for the pupal stage, and 10.3 °C and 185.18 DD for the total developmental time (Table 2).

Pupal mortality, parasitism and emergence rates

Pupal stage mortality of *A. hemara* is presented in Table 3. There was a highly significant difference in the mortality recorded at different temperatures ($\chi^2 = 106.50$, df = 3, $P < 0.0001$). The highest pupal mortality was recorded at 15 °C, but the lowest was recorded at 25 °C.

https://doi.org/10.1017/S0007485319000920 Published online by Cambridge University Press

Table 1. Developmental time (mean ± SE in days) of immature stages of *A. hemara* reared on *S. recurvalis*

	Sex					
	Male	Female				
Temperature	Egg-larval developmental time (days)		*W*	*t*	df	*P*
15 °C	28.20 ± 0.73^{aA}	28.50 ± 0.65^{aA}	11.5		1	0.794
20 °C	12.81 ± 0.09^{aB}	12.57 ± 0.08^{aB}	435.5		1	0.059
25 °C	7.31 ± 0.09^{bC}	7.70 ± 0.13^{aC}	619		1	0.024
30 °C	5.25 ± 0.08^{aD}	5.20 ± 0.07^{aD}	744		1	0.786
χ^2	115.39	86.783				
df	3	3				
P	<0.0001	<0.0001				
Pupal developmental time (days)						
15 °C	21.80 ± 1.74^{aA}	22.00 ± 0.41^{aA}		0.099	7	0.924
20 °C	7.88 ± 0.12^{bB}	8.96 ± 0.14^{aB}	952.5		1	<0.0001
25 °C	4.41 ± 0.09^{bC}	5.18 ± 0.11^{aC}	763.5		1	<0.0001
30 °C	3.84 ± 0.06^{aD}	3.93 ± 0.08^{aD}	827		1	0.385
χ^2	106.32	82.509				
df	3	3				
P	<0.0001	<0.0001				
Total developmental time (days)						
15 °C	50.00 ± 1.38^{aA}	50.50 ± 0.29^{aA}		0.36	4.35	0.739
20 °C	20.45 ± 0.1^{bB}	21.78 ± 0.17^{aB}	1003.5		1	0.0001
25 °C	11.72 ± 0.12^{bC}	12.88 ± 0.14^{aC}	811.5		1	0.0001
30 °C	9.10 ± 0.08^{aD}	9.13 ± 0.06^{aD}	812		1	0.476
χ^2	116.47	86.51				
df	3	3				
P	<0.0001	<0.0001				

Means followed by the same lower (upper) case letters in the same row (column for the same parameter) are not significantly different at $P < 0.05$ by the Wilcoxon rank sum test, two-sample *t*-test or Welch two-sample *t*-test (Dunnett test).

The successful parasitism rate (successful oviposition or realized fecundity) ($\chi^2 = 37.28$, df = 3, $P < 0.0001$) and adult emergence rate (fertility) ($\chi^2 = 106.50$, df = 3, $P < 0.0001$) were significantly affected by temperatures. The highest successful parasitism rate was obtained at 30 °C and the lowest at 15 °C. The highest adult emergence rate occurred at 25 °C and the lowest at 15 °C (Table 4).

Adult longevity and sex ratio of Apanteles hemara *at different temperatures*

Adult longevity of *A. hemara* was significantly influenced by temperature. Adult longevity decreased with increasing temperatures from 15 to 25 °C. An increase was, however, noted at 30 °C. There were no significant differences in the longevity of females and males at the four tested temperatures (Table 5).

There was no significant difference in the sex ratio at 15 °C ($\chi^2 = 0.09$, df = 1, $P = 0.757$) and at 25 °C ($\chi^2 = 0.29$, df = 1, $P = 0.59$). However, this was statistically different at 20 °C ($\chi^2 = 5.68$, df = 1, $P = 0.017$) and 30 °C ($\chi^2 = 9.8765$, df = 1, $P = 0.001$) where it was male biased (Table 6).

Female realized fecundity and survival

The realized fecundity of *A. hemara* was influenced by temperature and showed significant differences between the two tested temperatures ($W = 117$, df = 1, $P = 0.001$). The mean daily realized fecundity in terms of number of produced cocoons was 8.15 ± 1.03 at 20 °C and 2.41 ± 0.2 at 25 °C per female. No pre-oviposition period was observed. At 20 °C, the mean oviposition period was 12.20 ± 5.89, and at 25 °C, it was 11.61 ± 5.41 (figs 4 and 5).

Discussion

In biological control programmes, detailed information concerning thermal requirements and thresholds is useful in selecting natural enemies that are best adapted to conditions favouring target pests (Jervis and Copland, 1996). To the best of our knowledge, no data on the development of *A. hemara* on *S. recurvalis* at different temperatures are available. Results in the current study clearly showed that the development and the survival of *A. hemara* on *S. recurvalis* are highly significantly affected by

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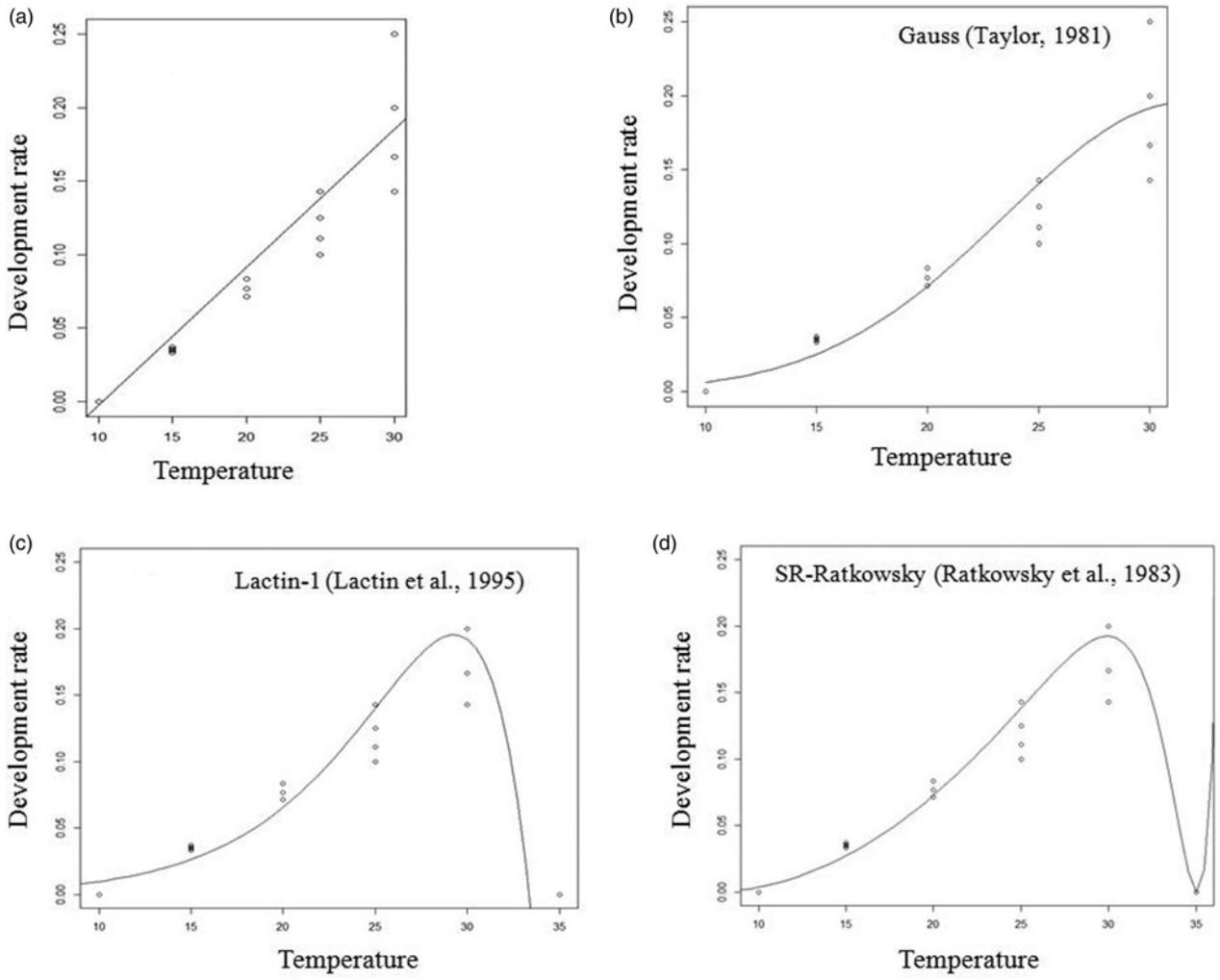

Figure 1. Linear (a), Taylor (b), Lactin-1 (c) and Ratkowsky (d) fitted models of the development rate (1/development duration) for the larval stage of *A. hemara*.

temperatures. Previous studies have shown the effect of temperatures on the development of various Braconid parasitoids (Cardona and Oatman, 1975; Zamani *et al.*, 2007; Htwe *et al.*, 2008). Insects, being poikilothermic, are particularly sensitive to their environmental temperature. *A. hemara* completed its development within range temperatures of 15–30 °C but not at 10 and 35 °C. Similar results were obtained by Cardona and Oatman (1975) who reported that *Apanteles subandinus* (Blanchard) (Hymenoptera: Braconidae) completed its development from egg to adult at temperatures of 15.5–32 °C but not at low temperatures of 11.2 °C. Similar developmental time trends were also obtained for *Apanteles taragamae* (Viereck) (Hymenoptera: Braconidae) for which a total developmental time of 12.3 days was obtained at 24 °C and 9.4 days at 30 °C (Dannon *et al.*, 2010). Our results on the developmental time are also comparable to the development of *Cotesia vestalis* (Haliday) (Hymenoptera: Braconidae) another Microgastrine parasitoid species at 20, 25, 30 and 35 °C which lasted for 19.6, 12.5 and 9.5 days respectively and no parasitoid pupae were recovered at 35 °C. However, at 15 °C, *C. vestalis* took 10 days less to complete its immature development as compared to *A. hemara* (Htwe *et al.*, 2008). The effect of temperature on an insect is explained by its interference with the metabolism, respiration, nervous system, endocrine system and heat shock protein capacity (Neven, 2000). At the lower extreme temperature, a delay in development occurs due to suboptimal feeding; but as the temperature increases, it is accompanied by an increase in the developmental rate up to a lethal limit, where the rate of metabolism decreases (Van Steenis, 1994).

In the current study, our findings showed that the developmental time of *A. hemara* was similar for females and males at only two of the four tested temperatures in the assay. These results are similar to previous studies on Microgastrinae. For instance, Esmat *et al.* (2017) reported that the differences between the duration of the immature developmental period of males and females of *Apanteles galleriae* (Wilkinson) (Hymenoptera: Braconidae) were not significant at 25, 27 and 30 °C but significant at 20 °C at a photoperiod of 0:24 (L:D). The developmental time of *A. taragamae* males and females on 2 days old larvae of *Maruca vitrata* (Fabricius) (Lepidoptera: Crambidae) at 25.3 ± 0.5 °C and 78.9 ± 5.6% relative humidity was not significantly different (Dannon *et al.*, 2010).

The selection of mathematical models that describe the relationship between temperatures and the developmental rate is essential. Linear functions fitted well the effect of temperature

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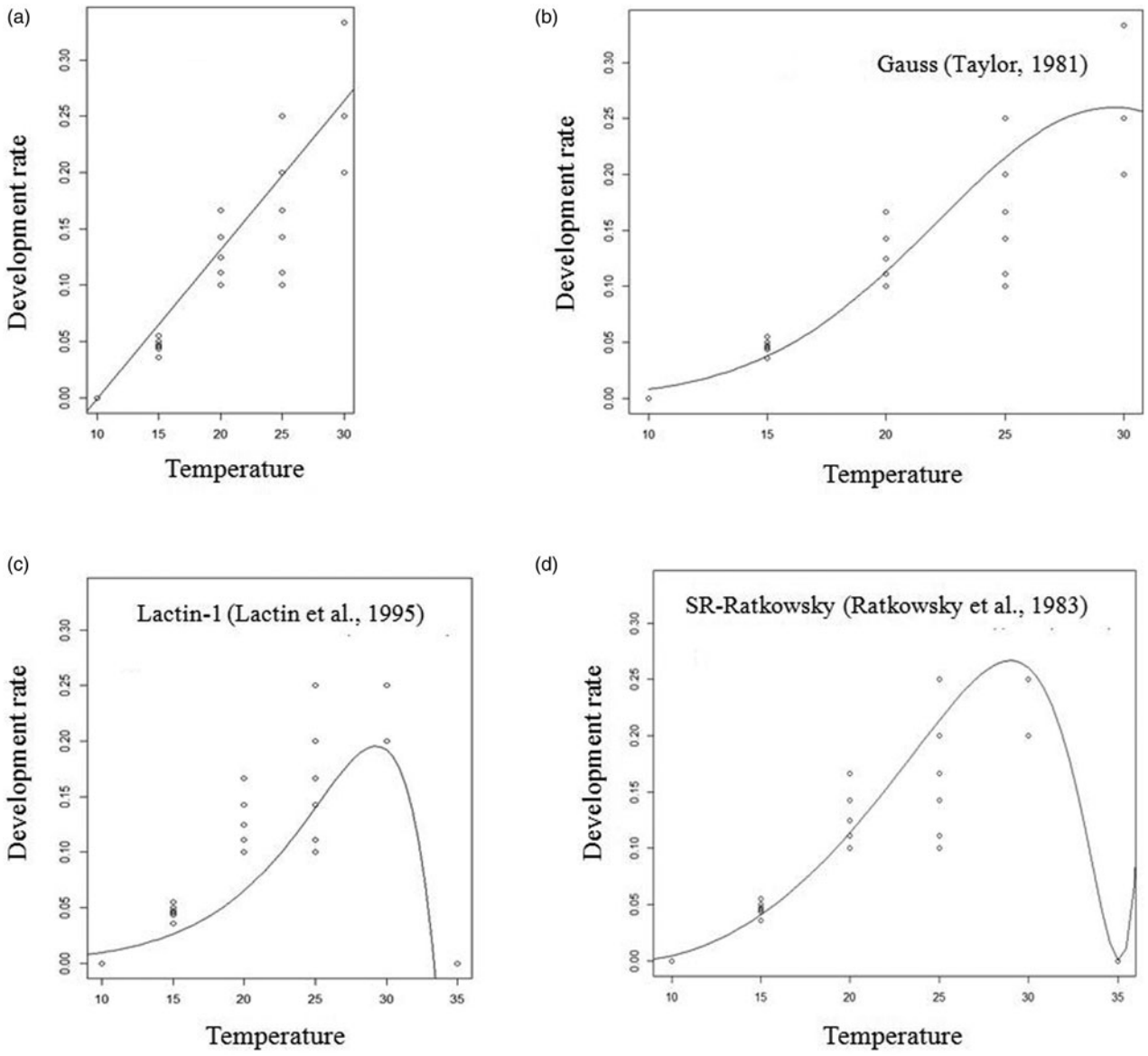

Figure 2. Linear (a), Taylor (b), Lactin-1 (c) and Ratkowsky (d) fitted models of the development rate (1/development duration) for the pupal stage of *A. hemara.*

on the development rate for all *A. hemara* immature stages (egg-larval and pupal) and the total developmental time, especially for temperature between 10 and 30 °C. However, for higher temperatures, the Lactin-1 model gave good results and allowed the calculation of the maximum temperature threshold. Although the coefficient of determination of the Taylor model was low, the parameters estimates were highly significant. The estimated values of optimum development temperature for the egg-larval and pupal stage were in accordance with the observed successful parasitism and adult emergence rates at 30 °C, though the parasitoid pupal mortality obtained at that temperature was a bit higher than at 25 °C. The lower developmental threshold of the immature stage of *S. recurvalis* reported in the literature is 10.4 °C (Lee *et al.*, 2013). The one of *A. hemara* obtained during this study (10.3 °C) is relatively close to the pests' lower threshold, and the parasitoid is therefore expected to keep in check the pest at lower temperature limits. However, the upper lethal temperature for *S. recurvalis* is 48.8 °C (Lee *et al.*, 2013), far above the upper thermal threshold of *A. hemara* (35.0 °C) leaving a huge gap where the pest will grow unchecked with temperatures above 35.0 °C. Such risk is fortunately reduced by the fact that the *S. recurvalis* optimal temperature range for growth is 25.0–30.0 °C (Lee *et al.*, 2013). However, global warming might favour the pest than the parasitoid.

The results of these experiments showed that temperature affected adult longevity. A constant decrease in adult parasitoid longevity as per the increase of the temperature (showing, therefore, an inverse relationship between longevity and temperature) is usually reported in other Braconidae species; for instance, in *Microplitis manila* (Ashmead) (Qiu *et al.*, 2012), *Chelonus inanitus* (L.) (Rechav, 1978), *Chelonus* sp. nr. *curvimaculatus* (Cameron) (Hentz *et al.*, 1998), *Bracon vulgaris* (Ashmead) (Ramalho *et al.*, 2011), *Chelonus murakatae* (Munakata) (Qureshi *et al.*, 2017) and *Psyttalia cosyrae* (Wilkinson) (Mohamed *et al.*, 2006). Our results, however, showed a partial difference at 30.0 °C where the longevity experienced an increase.

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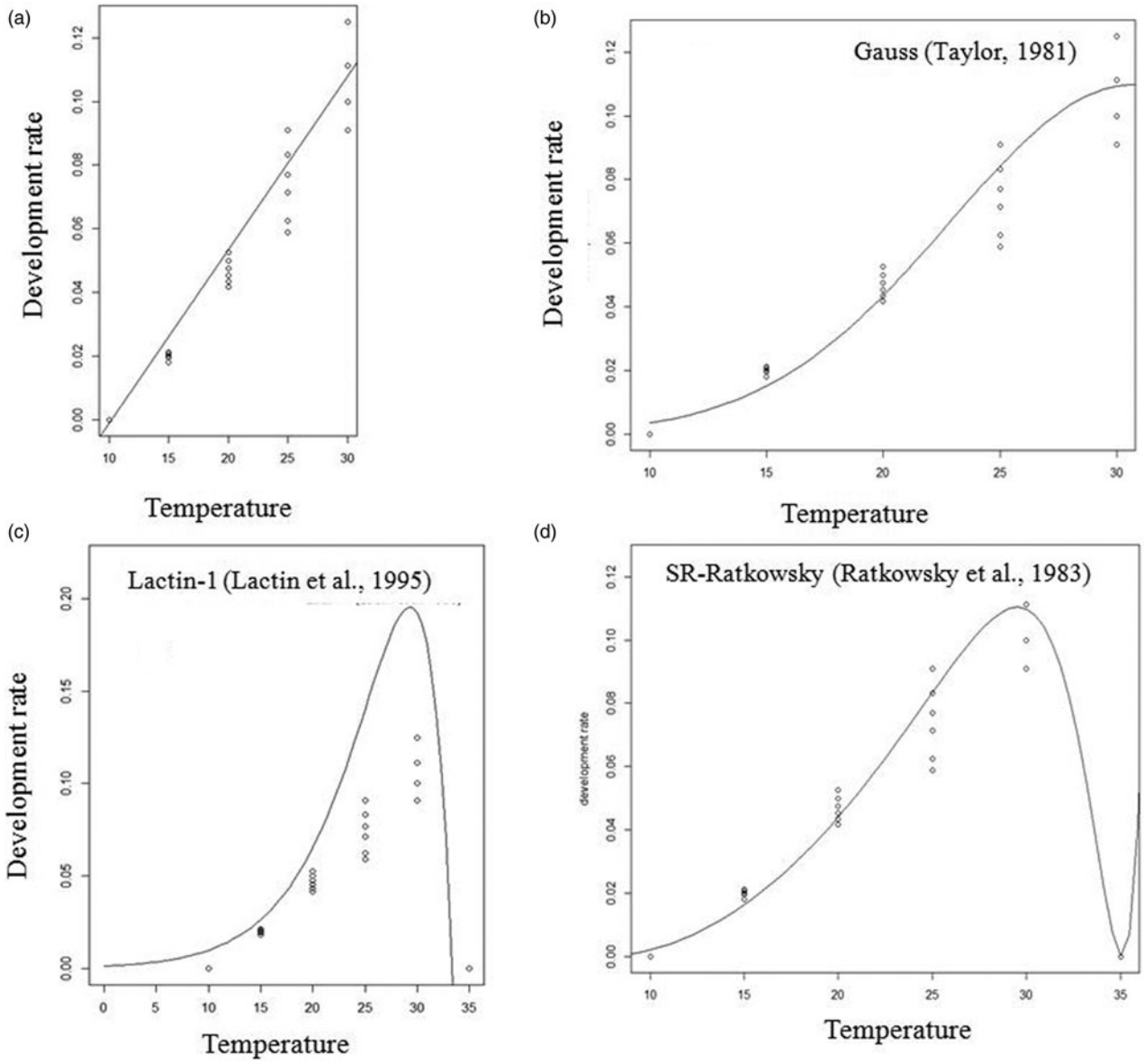

Figure 3. Linear (a), Taylor (b), Lactin-1 (c) and Ratkowsky (d) fitted models of the development rate (1/development duration) for the total developmental time of *A. hemara*.

There are some cases in Microgastrinae matching our findings, where a constant decrease was not always observed as the temperature increases such as in *A. galleriae* (Uçkan and Erginin, 2003), *C. murakatae* males (Qureshi *et al.*, 2017) and *B. vulgaris* males (Ramalho *et al.*, 2011).

The sex ratio was male-biased at 20 and 30 °C whereas it was balanced at 15 and 25 °C. The sex ratio is an important parameter when considering biological control agents. A female-biased sex ratio is sought as females are the ones responsible for attacking the pests through host feeding or oviposition (Berndt and Wratten, 2005; Chow and Heinz, 2005). Female parasitoids also cause the death of their host via nonreproductive effects (Abram *et al.*, 2019). In a study carried by Othim *et al.* (2017) on *A. hemara* at 25 ± 2 °C and 60 ± 10% RH, they obtained a female-biased sex ratio in a proportion of 59.09% which is close to 53.23% that was obtained in the current study at 25 °C. Our results on the sex ratio are also similar to the ones obtained in other Braconidae species where variable sex ratios were recorded according to the temperature. Mohamad *et al.* (2015) reported in *Ascogaster quadridentata* (Wesmael) a balanced sex ratio at 20, 25 and 30 °C but male-biased at 35 °C. The *Cotesia flavipes* (Cameron) sex ratio was female-biased at 30 °C, whereas more males emerged at lower temperatures (22 and 26 °C) (Jiang *et al.*, 2004). Hentz *et al.* (1998) found that the progeny of *Bracon hebetor* (Say) was female-biased at 20 °C but male-biased at 30 and 40°C. It was, however, unclear why in the present study, no clear gradient of temperature was obtained for male-biased and balanced sex ratio, and further studies are needed to elucidate this finding.

There was a significant difference in the daily realized fecundity registered at 20 and 25 °C, with 20 °C recording the highest fecundity. This result can be explained by the higher mortality

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Table 2. Model parameters of linear regressions, Taylor, Lactin-1 and Ratkowsky models for the temperature effect on *A. hemara* immature stages' development rate

Model	Formula	Parameters	Egg-larval stage	Pupal stage	Total development
Linear regression	$rT = a + bT$	a	−0.0966***	−0.1337***	−0.0556***
		b	0.0094***	0.0132***	0.0054***
		R^2	0.98	0.96	0.98
		K (DD)	106.38	75.76	185.18
		T_{min} (°C)	10.1	10.1	10.3
Taylor_81	$rT \sim R_m \times \exp(-1/2 \times ((T - T_m)/T_o)^2)$	R_m	0.20 ± 0.002***	0.26 ± 0.002***	0.1.10 ± 0.0007**
		T_m (°C)	31.8 ± 0.3***	29.6 ± 0.2***	30.8 ± 0.2***
		T_o (°C)	8.3 ± 0.2***	7.4 ± 0.2***	7.9 ± 0.1***
		R^2	0.057	0.005	0.116
		AIC	−2664.40	−2039.90	−3289.57
		BIC	−2648.20	−2023.70	−3273.37
Lactin1_95	$rT \sim \exp(aa \times T) - \exp(aa \times T_{max} - (T_{max} - T)/\Delta T)$	aa	0.22 ± 0.001***	0.20 ± 0.002***	0.21 ± 0.001***
		T_{max} (°C)	35.0 ± 0.0***	35.0 ± 0.0***	35.0 ± 0.0***
		ΔT (°C)	4.62 ± 0.03***	4.89 ± 0.047***	4.73 ± 0.03***
		R^2	0.27	0.16	0.49
		AIC	−3868.77	−2959.88	−4585.75
		BIC	−3851.02	−2942.125	−4568.00
Ratkowsky_83	$rT \sim (cc \times (T - T_1) \times (1 - \exp(k \times (T - T_2))))^2$	cc	0.02 ± 0.0003***	0.03 ± 0.0006***	0.02 ± 0.0001***
		T_1	7.1 ± 0.2***	7.6 ± 0.3***	7.3 ± 0.2***
		T_2	35.0 ± 0.1***	35. 1 ± 0. 1***	35.1 ± 0.1***
		k	0.49 ± 0.02***	0.35 ± 0.01***	0.42 ± 0.009***
		R^2	0.01	0.0006	0.035
		AIC	−4293.92	−3289.17	−5256.06
		BIC	−4271.73	−3266.98	−5233.87

Significance code: '***'P<0.0001. rT is the development rate, a: y intercept, b: slope, K: thermal constant (DD), T_{min}: lower development temperature threshold, T the temperature, R_m the maximum development rate, T_m the optimum temperature, T_o the rate at which the development rate falls away from T_m, T the temperature, aa, T_{max} and ΔT are fitted parameters, T_1 and T_2 the minimum and maximum temperatures at which the rate of growth is zero, cc the slope of the regression, k a constant and R^2 coefficient of determination.

Table 3. Effect of constant temperatures on *A. hemara* pupal morality when reared on *S. recurvalis*

Temperature	Pupal mortality (%)
15 °C	84.48[a]
20 °C	24.18[b]
25 °C	1.59[c]
30 °C	25.45[b]
χ^2	106.50
df	3
P	<0.0001

Means followed by the same letter in the same column were not significantly different by the proportion test, $P < 0.05$.

Table 4. Effect of constant temperatures on *A. hemara* parasitism and emergence rates when reared on *S. recurvalis*

Temperature	Successful parasitism (%)	Emergence (%)
15 °C	29.00 (n* = 58)[a]	15.52 (n = 9)[a]
20 °C	45.50 (n = 91)[b]	75.82 (n = 69)[b]
25 °C	31.50 (n = 63)[a]	98.41 (n = 62)[c]
30 °C	55.00 (n = 110)[b]	74.55 (n = 82)[d]
χ^2	37.28	106.50
df	3	3
P	<0.0001	<0.0001

* n represents the number of collected cocoons and emerged adults.
Means followed by the same letter in the same column were not significantly different by the proportion test, $P < 0.05$.

registered at the larval stage at 25 °C as compared to 20 °C and the higher number of eggs deposited at 20 °C. Daily fecundity recorded in *A. taragamae* varied from 5.5 at 20 °C to 1.2 at 30 °C (Dannon *et al.*, 2010), results which are not far from what we observed in the current study in *A. hemara,* and support the idea that the daily fecundity is affected by temperature. The

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Table 5. Effect of constant temperatures on adult longevity (mean ± SE in days) of *A. hemara* when reared on *S. recurvalis*

	Sex					
	Male	Female				
Temperature	Adult longevity (days)		*W*	*t*	df	*P*
15 °C	24.6 ± 5.63^{aA}	22.5 ± 8.77^{aAB}		−0.21	7	0.840
20 °C	15.57 ± 1.59^{aB}	14.81 ± 1.96^{aA}	525			0.6093
25 °C	9.41 ± 0.83^{aC}	9.88 ± 0.92^{aC}		0.37	60	0.7115
30 °C	18.96 ± 1.2^{aA}	20.97 ± 1.5^{aB}	878			0.2704
χ^2	24.4996	22.5539				
df	3	3				
P	<0.0001	<0.0001				

Means followed by the same lower (upper) case letters in the same row (column) are not significantly different at $P < 0.05$ by the Wilcoxon rank sum test or two-sample *t* test (Dunnett test).

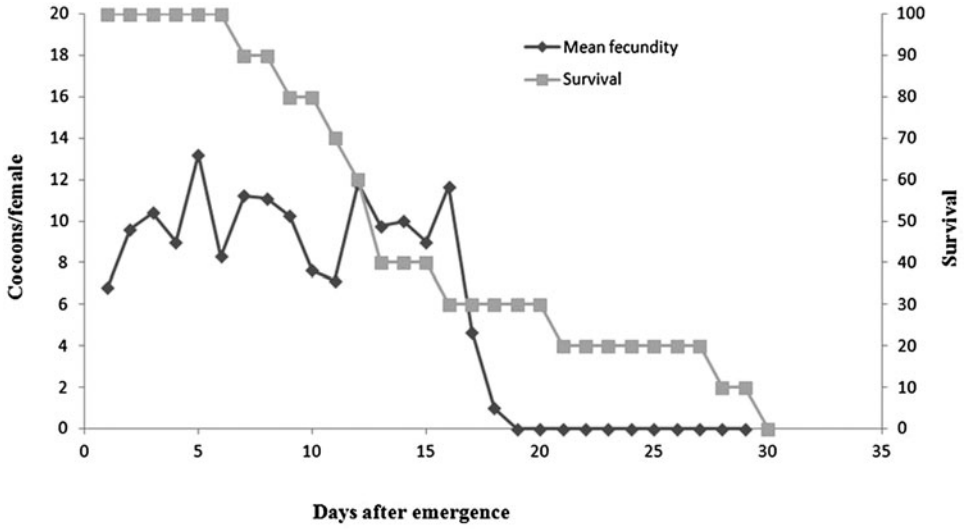

Figure 4. Age-specific reproduction and survival of adult females of *A. hemara* reared on *S. recurvalis* at 20 °C, 60–70% relative humidity and 12:12 h (light:dark) photoperiod.

Table 6. Effect of constant temperatures on the *A. hemara* sex ratio when reared on *S. recurvalis*

Temperatures (°C)	Sex ratio (%)		χ^2	df	*P*
	Male	Female			
15	55.56^{a}	44.44^{a}	0.09	1	0.757
20	60.87^{a}	39.13^{b}	5.68	1	0.017
25	46.77^{a}	53.23^{a}	0.29	1	0.59
30	62.96^{a}	37.04^{b}	9.8765	1	0.001

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

extended longevity of the female at 20 °C is translated into longer post-oviposition period, meaning that *A. hemara* lays most of their eggs in the first 2 weeks following their emergence. Şengonca and Peters (1993) showed that the *Cotesia rubecula* (Marsh.) (Hymenoptera: Braconidae) oviposition period lasts about 17 days which is similar to the results we obtained in this study. No pre-oviposition was observed during this experiment on *A. hemara*. The absence of pre-oviposition period was reported in other Microgastrinae species such as *Pseudapanteles dignus* (Muesebeck), a primary parasitoid of the tomato pinworm *Tuta absoluta* (Meyrick) (Lepidoptera: Gelechiidae) (Cardona and Oatman, 1971), *Apanteles machaeralis* (Wilkinson) a parasitoid of *Diaphania indica* (Saunders) (Lepidoptera: Pyralidae) (Peter and David, 1990), *Apanteles s.* (Blanchard) (Cardona and Oatman, 1975), *C. rubecula* (Şengonca and Peters, 1993) and *Glyptapanteles thompsoni* (Lyle) (Hymenoptera: Braconidae) (Vance, 1931).

Conclusion

This study is the first to report the effect of temperature on *A. hemara*, an important parasitoid of amaranth lepidopteran defoliator, *S. recurvalis*. The study showed that temperature has a strong

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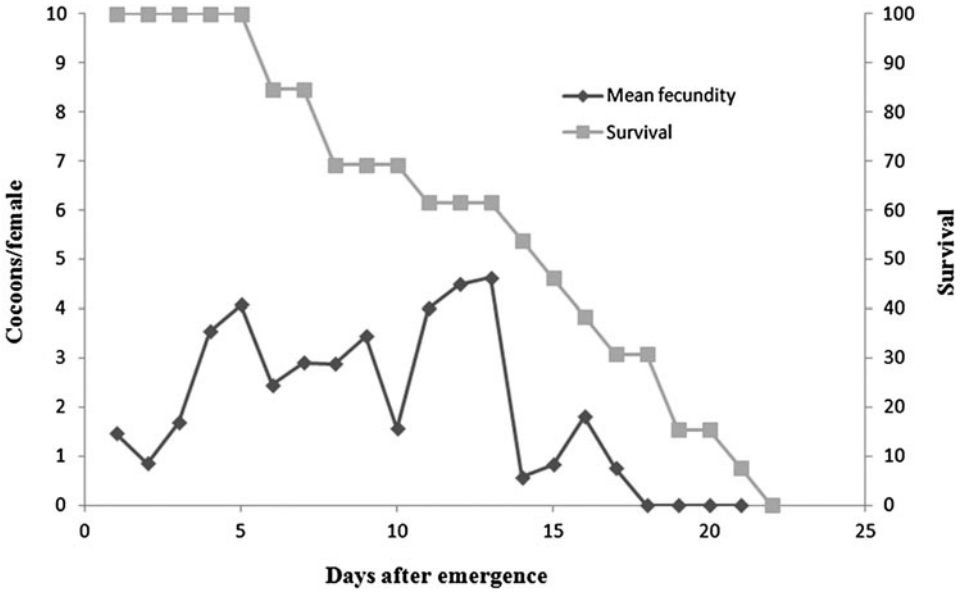

Figure 5. Age-specific reproduction and survival of adult females of *A. hemara* reared on *S. recurvalis* at 25 °C, 60–70% relative humidity and 12:12 h (light:dark) photoperiod.

effect on the development rate, mortality, sex ratio, fecundity and longevity of *A. hemara*. This parasitoid has the estimated optimal total development at 30.8 °C, which gives an indication of the optimal conditions for mass rearing. It also provides the first data on the temperature range suitable for field releases in augmentative biological control. Moreover, this study has contributed to the deeper understanding of the biology of *A. hemara* and has formed a basis for future phenology modelling works such as validation of the model under fluctuating temperatures, forecasting phenology of *A. hemara* with existing climate data especially temperature. This will allow to determine the number of generations of the parasitoid per year in a given agro-ecological zone base on its degree-days requirement, and to know which period of the year the parasitoid will be likely absent. Also, a comparative study of thermal requirements between the pest and the natural enemy is warranted.

Acknowledgements. The present study was funded by the German Federal Ministry for Economic Cooperation and Development (BMZ). We gratefully acknowledge also the financial support for the core research agenda of *icipe* by UK Aid from the UK Government; Swedish International Development Cooperation Agency (Sida); the Swiss Agency for Development and Cooperation (SDC); and the Kenyan Government. The first author received a scholarship from the German Academic Exchange Service (DAAD) through *icipe* Capacity Building Program (ARPPIS). The authors express their gratitude to the project team for their technical assistance.

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https://doi.org/10.1017/S0007485319000920 Published online by Cambridge University Press