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Effects of different temperatures on the life history of *Evania appendigaster* L. (Hymenoptera: Evaniidae), a solitary oothecal parasitoid of *Periplaneta americana* L. (Dictyoptera: Blattidae)

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ABSTRACT

The influence of temperatures on the life parameters of the solitary oothecal parasitoid *Evania appendigaster*, was investigated in the laboratory. Parasitized oothecae of *Periplaneta americana* were left to develop under seven constant temperatures: 15, 17, 20, 25, 30, 35, and 40 °C. At the end, we found that: (i) *E. appendigaster* was able to complete development within the temperature range of 17–34 °C; (ii) mean adult longevity decreased as temperature increased, with the temperature of 40 °C being fatal in a matter of hours; (iii) males lived longer than females between 15 and 30 °C; (iv) adult emergence rate was the highest at 25 °C, and (v) no wasps emerged at 15 or 40 °C. Non-emerged oothecae contained either unhatched eggs or dead larvae. We determined the theoretical lower developmental threshold and thermal constant for the complete development as 12.9 °C and 584.8 day-degrees for males, and 13.1 °C and 588.2 day-degrees for females, respectively. A good balance between faster development, maximum adult longevity and good egg viability was obtained between 25–30 °C, and that would be the best temperature range for rearing *E. appendigaster*.

1. Introduction

The American cockroach, *Periplaneta americana* L., is the largest common peridomestic insect in tropical and subtropical regions of the world (Roth and Willis, 1960). Cockroaches hold considerable economic and public health importance because they are in close contact with human wastes and pathogens, and have the habit of invading homes and commercial establishments (Brenner et al., 1987; Ebeling, 1978). A number of natural enemies including parasites, predators, and symbionts attack them (Roth and Willis, 1960). Several hymenopterans attack cockroaches, for example the parasitic wasps *Ampulex compressa* F., *Evania appendigaster* (L.) and *Aprostocetus* (*Tetrastichus*) *hagenowii* (Ratz.) (Cameron, 1955; Lebeck, 1991; Suiter et al., 1998).

Temperature is a key environmental factor affecting many life parameters of insects, as they are poikilothermic organisms (Rinehart et al., 2000; Hoffmann et al., 2003), and extreme temperatures can be detrimental to several fitness traits of the insects (Rinehart et al., 2000). For example, the development time and growth rate of each insect species will depend on its genetic and physiological status, and also on the prevailing environmental conditions, the most important of which being temperature (Nakahara et al., 2000; Davidowitz and Nijhout, 2004; Trudgill et al., 2005; Nijhout et al., 2006). Insect development speed slows down as temperature drops until a complete halt at the so called 'lower threshold' (LTT, or 'base temperature'). Development also stops at temperatures beyond the 'upper threshold', and is fastest at an intermediary optimal temperature (see Chong and Oetting (2006)). These temperature thresholds are therefore ambient barriers limiting insect development. Every insect species requires a certain total number of day-degrees (DD)—the accumulated amount of degrees Celsius over the lower threshold over the days—to complete its development. This amount of DD is known as the 'thermal constant' (*K*) (Wigglesworth, 1972).

E. appendigaster occurs in tropical and subtropical world regions (Stange, 1978), and parasitizes oothecae of synanthropic cockroaches, such as some species of *Blatta* and *Periplaneta* (Deans, 2005; Férnandez and Sharkey, 2006). This parasitic wasp lays one egg inside the ootheca from which hatches a larva that consumes all other cockroach embryos/nymphs inside.

The scientific literature on the biology of this wasp is scarce and fragmented. Cameron (1955), Lebeck (1991), Edmunds (1955), Piper et al. (1978) and Hagenbuch et al. (1988) proposed using *E. appendigaster* for the biological control of urban cockroach populations. A description of oviposition behavior was given by Haber

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(1920), while Crosskey (1951) visited aspects of morphology, taxonomy and biology. Cameron (1957) studied the general biology of *E. appendigaster* including foraging, oviposition and morphology of the developmental stages, and Kumarasinghe and Edirisinghe (1986) evaluated the wasps' ability to discriminate between parasitised and unparasitised hosts and determined parasitism rates at various ages. More recently, Yeh and Mu (1994) and Yeh et al. (2000) further analysed oviposition behavior, and Fox and Bressan-Nascimento (2006) quantified some biological parameters of this wasp as related with host density. No studies focused on the effects of temperature on the adult life of *E. appendigaster*.

Thus, this paper investigated the effects of different temperatures on the life parameters of *E. appendigaster*. The results obtained are useful for optimising rearing conditions of these parasitoids and can help predicting population dynamics of these wasps in the field.

2. Materials and methods

2.1. Insect colonies

A stock colony of *P. americana* was established from field-collected cockroaches in a rearing room at 23–31 °C, relative humidity of 50–85%, and exposed to a photoperiod of L14:D10.

A colony of *E. appendigaster* was established in a separate room at 26 ± 2.2 °C and relative humidity 69 ± 3%, and same photoperiod as above. In all described procedures randomly chosen 0–24 h-old evaniid wasps were used. Further details on the rearing of insects in Fox and Bressan-Nascimento (2006) and Bressan-Nascimento et al. (2008).

2.2. Experiments

2.2.1. Effects of temperature on the biological parameters of *E. appendigaster*

The wasps were kept in male–female cohorts inside 18 × 13 × 14-cm plastic boxes with one 11-cm holes on each side. One hole was sealed with a piece of veil for respiration and the other attached with a cloth sleeve for manipulation. The plastic boxes were held inside incubators set to the constant temperatures of 15, 17, 20, 25, 30, 35, or 40 °C (±1 °C) and maintained at 70 ± 2% of relative humidity under a 14L:10D photoperiod. The wasps were given 20% sucrose solution and tap water ad libitum, and two 0–48 h-old oothecae. Twelve simultaneous replicates were prepared for each different temperature test. Every 48 h the presented oothecae were replaced until the female wasp was dead. The retrieved oothecae were stored individually in 3 × 10-cm glass flasks. The flasks were then held in the parasitoid rearing room and inspected daily for emerging insects.

Oothecae that failed to emerge after 3–4 months were dissected, and any non-emerged parasite larvae or adults, or cockroach nymphs found were recorded. Oothecae found with dead parasites inside were considered parasitized.

The following parameters in each treatment were measured: (1) longevity of males and females (in days from emergence from the ootheca to death); (2) female ratio (number of females emerged divided by total brood); (3) parasitism rate (the number emerged plus non-emerged (dead) larvae divided by total amount of exposed oothecae × 100); (4) emergence rate (number emerged divided by total amount of exposed oothecae × 100); (5) viability (number emerged divided by total number of parasitized oothecae × 100); and (6) developmental time in days (from oothecae exposure to emergence).

2.2.2. Effects of constant temperatures on the oviposition of *E. appendigaster*

To check the influence of temperature on the oviposition by *E. appendigaster*, the same experimental protocol described above was repeated, with the oothecae being exposed and replaced every 48 h only during the first fifteen days of the females' lifetime ($N = 12$) as this is the period during which *E. appendigaster* females display their greatest reproductive efficiency (Fox and Bressan-Nascimento, 2006). A group of 12 replicates was kept in the insect rearing room as controls. The replaced oothecae were carefully dissected with a fine forceps in saline solution to see if they contained parasite eggs inside. The number of eggs found was recorded, and cases in which more than one egg was found were considered superparasitism.

The wasp eggs found were carefully transferred to glass Petri dishes with 5 ml of physiological saline solution wherein they were kept and inspected until hatching. To determine if the constant temperature was killing the embryos before hatching, half of the eggs were held in the same test temperatures and the other half were held in the insect rearing room. From this experiment, we determined: (i) attack rate (number of oothecae with wasp eggs divided by the total number of oothecae × 100); (ii) egg viability (number of hatched eggs divided by the total number of eggs found × 100) and (iii) post-oviposition development time (period in days between oviposition and hatching) for each tested constant temperature.

2.3. Data analysis

Differences in life parameters under the different temperatures were detected with nonparametric Kruskal–Wallis test and means were separated using Dunn's multiple range test. Life span and development time of male and female wasps were compared within each temperature treatment by Mann–Whitney test. Means were considered significantly different if $P < 0.05$. All statistical analyses were made using the software GraphPad Instat v. 3.0.

The development rate (Dr) at each temperature was determined based on the developmental time (D) described above by dividing $1/D$. The development rate for each temperature was plotted and fitted to linear and non-linear models. The linear model was used to estimate the lower temperature threshold (LTT) and a thermal constant (K). The lower temperature threshold was assessed using data within the mid-range temperature treatments (17–30 °C) and a linear equation (Wigglesworth, 1972): $Dr = a + bT$ where the development rate (Dr) is a linear function of temperature in degrees Celsius, and a and b are regression parameters fitted to the data. The LTT was estimated based on the intersection of the regression curve with its abscissa, where the development rate (Dr) approaches zero (LTT = $-a/b$). The thermal constant was obtained from equation: $K = D\ (t - \mathrm{LTT})$ wherein K = thermal constant, D = development period (days), t = temperature in which the insect developed, and LTT = lower thermal threshold (see Wigglesworth (1972)). The necessary amount of day-degrees was based on the results of egg development and adult emergence. Because the linear model cannot estimate the upper temperature threshold (UTT) we made use of the non-linear model described by Wang et al. (1982), expressed as: $Dr = H/1 + \exp(-rm\ (T - To))\ (1 - \exp(-T - \mathrm{LTT/B}))\ (1 - \exp(-\mathrm{UTT} - T/B))$, where Dr is the development rate at the tested temperature T, H is the value of the upper asymptote of the curve, rm is the exponential increase rate, To is the optimum temperature for development, LTT is the lower thermal threshold, UTT is the upper thermal threshold, and B is the amount of degrees Celsius (width) between the upper and lower thresholds. The non-linear model was fitted to the