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Effect of temperature on pupa development and sexual maturity of laboratory *Anastrepha obliqua* adults

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Abstract

The effect of four temperatures (18, 20, 25 and 30°C) on pupa development and sexual maturity of *Anastrepha obliqua* adults was investigated under laboratory conditions. The results showed that the duration of the pupal stage decreased with an increase in temperature (29, 25, 13 and 12 days, respectively), and maintaining the pupae at 18°C and 20°C results in a low percentage of pupation, pupa weight loss and lesser flying ability. However, it significantly favored sexual behavior, a higher proportion of sexual calls and matings. While enhanced pupa development was observed at a temperature of 30°C, adults had low sexual efficiency, as well as a lower proportion of calls and matings. Gas chromatography-mass spectrometry (GC-MS) analysis of male volatiles showed that the amount of (*Z*,*E*)-α-farnesene did not vary among males from pupae reared at different temperatures; however, less (*E*,*E*)-α-farnesene was emitted by males obtain from pupa reared at 30°C. Male flies kept at 30°C during their larval stage had more (*Z*)-3-nonenol and, also, an unknown compound was detected. The fecundity of the females was higher at low temperatures. Regarding fertility, no significant differences were found between temperatures. The optimal temperature on pupa development was 25°C when males displayed ideal attributes for rearing purposes.

Keywords: *Anastrepha obliqua*, mass-rearing, pupae, SIT, temperature

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Introduction

The West Indian fruit fly, *Anastrepha obliqua* (Macquart) (Diptera: Tephritidae), is distributed throughout the Americas and can be found from the southern United States to Brazil (Hernández-Ortiz & Aluja, 1993). In Mexico, it is the second most economically important species affecting mango (*Mangifera indica* L.) production and marketing (Aluja, 1994). Control of this pest is carried out through integrated pest management, in which the Sterile Insect Technique (SIT) is the key element (Rull-Gabayet *et al*., 1996; Reyes *et al*., 2000; Enkerlin, 2005). However, SIT success depends on the quality of the sterile insects released, which is closely related to optimal environmental conditions for development during the mass-rearing process (Schwartz *et al*., 1985; Vargas, 1989; Artiaga-López *et al*., 2004; Klassen & Curtis, 2005; Cáceres *et al*., 2007). Temperature is one of the most important environmental factors in insect mass-rearing, affecting development time, maturation and survival (Kemp & Bosch, 2005; Kalaitzaki *et al*., 2007). In fruit flies, it is directly related to pupa development time and adult emergence (Vargas *et al*., 1996,

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2000; Taufer *et al.*, 2000; Donoso *et al.*, 2003). For *Ceratitis capitata* (Wied.), it has been determined that the optimum conditions for the development of pupae is between 20°C and 25°C with 75% and 90% RH (Langley *et al.*, 1972). In *Anastrepha ludens* (Loew) and *Anastrepha suspensa* (Wied.), it is reported that, under relaxed rearing conditions (25°C), pupa weight increases and adult mating ability is improved (Prescott & Baranowski, 1971; Meza *et al.*, 2005; Orozco-Dávila *et al.*, 2008). Moreover, pupa eye colour is used as an indicator of pupa maturation, and the rate of change is sensitive to temperature variations (Resilva *et al.*, 2007). Despite an abundance of research dealing with the effect of temperature on the biology of fruit flies, little is known of the effect of temperature on adult performance. The main aim of this study was to investigate the effect of temperature on *A. obliqua* pupal development, production of sexual pheromone compounds, sexual calling propensity, male mating competitiveness, and female fecundity and fertility.

Material and methods

Biological material

Eight-day-old mass-reared larvae (close to pupation) were obtained from the Moscafrut facility, located in Metapa de Dominguez, Chiapas, Mexico. Flies were reared under standard operational protocol (Artiaga-López *et al.*, 2004) for about 128 generations. Wild flies were obtained as larvae from infested *Spondias mombin* L. fruit collected in the Soconusco Region, Chiapas, Mexico.

Experimental protocol

For pupation, batches of 1000 third instar larvae were placed in 22 × 12 × 3.5-cm plastic trays with 100 g of vermiculite. The trays were placed in different environmental chambers (Percival Scientific No. Series 02-EC-184-007) at 18, 20, 25 and 30°C and 65–85% RH until adult emergence. Once the adults emerged, they were sorted by sex and placed in 30 × 30 × 30-cm glass cages, covered on one side by a 2-mm tull mesh and kept in separated rooms. Adults were fed *ad libitum* with a mixture of enzymatically hydrolyzed yeast (ICN Biomedical, Aurora, OH, USA) and sucrose in a 1:3 ratio, and water was provided in 500-ml plastic bottles covered with a cotton wick. These adult cages were kept in the laboratory at a temperature of 25 ± 1°C, 65 ± 5% RH, and 12:12 L:D photoperiod (07:00–19:00 h light, and 550 ± 50 lux light intensity).

Field cage tests were carried out in a mango (*M. indica* L.) cv. Ataulfo orchard located in the municipality of Tapachula (14°10–15°20 N, 92°10–93°10 W, 180 m altitude), Chiapas, Mexico. The temperature in the orchard fluctuated from 18°C to 33°C and RH from 50% to 70%.

Effect of temperature on pupation and pupae weight

Following the exposure of 1000-larvae samples to each temperature treatment for 24 h, pupation percentage was calculated. Ten samples of 100 pupae, each from different batches of larvae, were extracted for each temperature treatment. In accordance with the method described in the FAO/IAEA/USDA manual, each sample of pupae was weighed on an analytical balance (Ohaus Model AP2105, Pine Brook, NJ, USA). Pupation percentage and mean pupal weight were estimated following the procedures described in the Quality Control Manual (FAO/IAEA/ USDA, 2003).

Pupal development time, adult emergence and flying ability

Pupal development time was estimated as the number of days from pupation to adult emergence. Pupa viability was determined from 100-pupae samples. Twenty replicates for each temperature were done. The pupae from each sample were placed in 100 × 15-mm Petri dishes inside 8.9 cm diameter × 10 cm height black PVC tubes. The inner wall of each tube was coated with talcum powder to prevent flies from escaping by walking out of the tube. The tubes were placed inside a field cage (3 m diameter × 2 m height) (Calkins & Webb, 1983; Chambers *et al.*, 1983) for six days. After six days, the number of non-emerged pupae and non-flying adults was recorded and the percentage of fliers was estimated (FAO/IAEA/ USDA, 2003).

Male sexual maturity

To assess male sexual maturity, a two-factor experimental design was used. The first factor was temperature (18, 20, 25 and 30°C) and the second factor was age (4, 6, 8, 10 and 12 days). There were a total of 20 treatments, each replicated 20 times, using 30 males placed in 30 × 30 × 30-cm glass cages. Observations were made every half hour; calling behavior was used as a signal of sexual maturation and was determined by vigorous wing fanning, everted prostiger and puffed pleural glands. Observations were carried out from 07:00 to 11:00 h, when sexual activity in *A. obliqua* is at its peak (Aluja & Birke, 1993). Laboratory temperature was 25 ± 2°C.

Collection of volatiles emitted by males

Samples of ten 8-day-old males were used for volatile collections. Collections were made between 08:00 and 10:00 h. Twenty replicates for each temperature from different cohorts were carried out. Volatiles emitted by calling *A. obliqua* males were collected using the system described by Heath & Manukian (1992). Collected volatiles were eluted with 200 µl methylene chloride. Each sample was deposited in a vial, sealed and stored at −20°C until required in the chemical analysis. Volatile collection was carried out in the laboratory at a temperature of 25 ± 2°C, 50–60% RH and lighting of 700 lux provided by fluorescent lamps placed 3 m from the collection tubes.

Chemical analysis

Volatile analysis was carried out using a Varian Star 3400 CX gas chromatograph coupled to a Varian Saturn 4D mass spectrometer, using helium as a gas carrier, with an initial temperature of 50°C maintained for two minutes then increased to 15°C min^{-1}, until reaching 280°C. Before injecting each sample, 20 µl of tridecane as internal standard was added to obtain a concentration of 100 ng μl^{-1}. Quantification of the four compounds present in the blend was done by measuring the area of the chromatogram peaks and comparing it with the internal standard. The compounds were identified using their retention times, Kovat index (KI) and mass spectra, and then comparing these data with those of synthetic standards. Synthetic standards of farnesene (mixture of isomers that includes (*E*,*E*)-α-farnesene and (*Z*,*E*)-α-farnesene) and (*Z*)-3-nonenol

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were supplied by Aldrich (Toluca, Mexico). Amounts of volatile compounds released by males are reported in nanograms per male per hour.

Sexual competitiveness

Twenty mass-reared males from each temperature treatment, 20 wild males and 50 wild females (a total of 150 insects) were released in each field cage (Calkins & Webb, 1983; Chambers *et al*., 1983). Mass-reared males were eight days old and wild flies were 15 days old. Mango trees (1.5 m high) were placed inside each field cage (Meza-Hernández *et al*., 2002).

For identification, males from each treatment were marked with a numbered (Arial type size 3) small paper tag (2 mm in diameter) glued onto the flies' thorax (Meza & Díaz-Fleisher, 2006) 48 h previous to the experiment conducted between 07:00 and 11:00 h. The number and type of matings were recorded. Each temperature at which males developed from pupae was considered a treatment; 25°C was considered the control. Six replicates per treatment were carried out.

Fecundity and fertility

Fecundity was estimated as the number of eggs per female per day. Ten sexually mature pairs (eight days old) were placed in 20 × 20 × 20-cm plexiglass cages at 25 ± 2°C, 65 ± 5% HR and 550 ± 50 lux. An oviposition panel (cylindrical, plastic, 4 cm long × 5.5 cm diameter, decked at one end with tergal white fabric as an oviposition substrate and coated with silicon on the inside) filled with distilled water stained with artificial green dye (McCormick of Mexico, S.A. de C.V.), was placed at the top of each cage. The eggs laid were collected daily over a period of ten days. To determine egg hatch, the eggs were incubated on a wet cloth, placed over a water saturated sponge in a 100 × 15-mm plastic Petri dish and maintained at 25°C for five days, considering fertility as the percentage of hatched eggs. Each treatment was replicated ten times.

Statistical analyses

Data were analyzed by analysis of variance (ANOVA) (Ott & Longnecker, 2001) followed by a Tukey separation of means test. The data on percentage of pupation, viability and egg hatch were transformed to arcsine of the square root of the proportion ($\chi = \mathrm{Sen}^{-1}\sqrt{\chi}$, where χ was the original proportion (percentage/100)) (Zar, 1999). When a Bartlett test (Zar, 1999) for equal variances was not significant for arcsine transformed data ($P \leq 0.05$), a one way analysis of variance was applied; and the separation of means was performed by applying a Fisher PLSD test. A two-way ANOVA was used to analyze the effect of temperature on the calling behavior of males and on the quantity of released volatile compounds. Means were compared by the Tukey test ($P \leq 0.05$). StatView 5.01 (SAS Institute, 2001) was used for all the analysis.

Results

Effect of temperature on pupation and pupa weight

Differences in larval pupation were significant (F = 12.09; df = 3, 40; $P < 0.05$) (table 1). The lowest percentage of larva pupation was recorded when pupae developed at 18°C, while the percentages were higher at 20, 25 and 30°C, but the differences were not significant. Differences in pupa weight loss were also significant (F = 58.12; df = 3, 98; $P < 0.05$) (table 1). The greatest loss occurred at 18°C, followed by 20°C. The lowest loss was observed at 25°C and 30°C.

Table 1. Percentage of pupation and weight loss experienced by *A. obliqua* pupae at different temperatures.

Temperature (°C)	Pupation (% ± SE)	Pupa weight loss (mg ± SE)
18	64.12 ± 1.91 b	7.8 ± 0.21 a
20	76.51 ± 1.52 a	5.95 ± 0.23 b
25	76.38 ± 2.08 a	4.53 ± 0.2 c
30	74.76 ± 1.51 a	4.5 ± 0.12 c

Different letters within columns (a, b, c) indicate significant differences ($P < 0.05$).

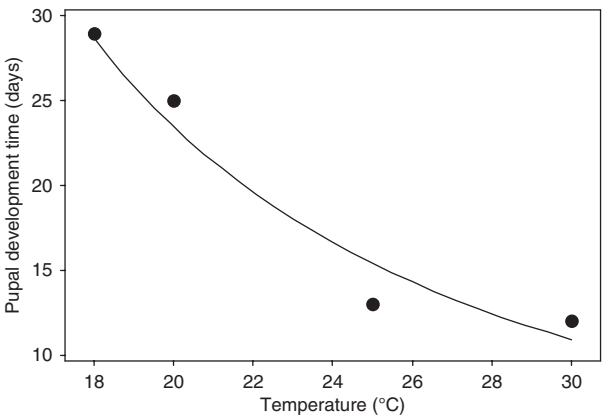

Fig. 1. Regression of temperature on *A. obliqua* pupal development time ($r^2 = 93.1$; F = 26.89; $P = 0.035$).

Pupal development time, adult emergence and flying ability

The duration of the pupal stage decreased with an increase in temperature (fig. 1), displayed by the regression equation log y = 3.84–1.89 log(x), $r^2 = 93.1$ (F = 26.89; df = 1, 2; $P = 0.035$). The greater emergence percentages were observed at 25°C and 30°C, while the lowest was at 18°C; the differences were significant (F = 218.57; df = 3, 97; $P < 0.05$). The highest percentage of flyers occurred at 25°C and the lowest at 18°C and 20°C; again the differences were significant (F = 196.94; df = 3, 97; $P < 0.05$) (table 2).

Male sexual maturity

Male sexual maturity, expressed by sexual calling, was observed as of six days of age, regardless of temperature treatment. Calling behavior was significantly affected by temperature (F = 5.33; df = 3, 144; $P < 0.05$) by age (F = 48.51; df = 3, 144; $P < 0.05$), and the temperature-age interaction was significant (F = 3.68; df = 9, 144; $P < 0.05$). Six-day-old males displayed an increase in activity at 18°C and 20°C. On the eighth day, males reared at 30°C showed reduced calling propensity. On the tenth day, males developed at 18°C showed the lowest calling propensity. On day 12, the flies that developed at 20°C were those that exhibited greatest sexual activity (fig. 2).

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Table 2. Emergence percentage and percentage of *A. obliqua* flyers (emerged flies capable of flight) exposed to different temperatures during their pupal stage.

Temperature (°C)	Emergence (% ± SE)	Flyers (% ± SE)
18	36.83 ± 1.48 a	33.29 ± 1.48 a
20	41.44 ± 1.99 b	36.92 ± 1.63 a
25	74.81 ± 0.56 c	69.87 ± 0.67 b
30	71.49 ± 0.77 c	59.95 ± 1.07 c

Different letters within columns (a, b, c) indicate significant differences ($P < 0.05$).

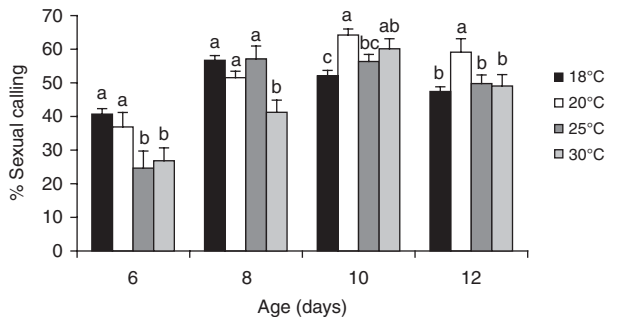

Fig. 2. Sexual calling of *A. obliqua* males from pupae developed at different temperatures. Different letters above bars indicate significant differences ($P < 0.05$).

Volatiles emitted by males

Gas chromatography-mass spectrometry (GC-MS) analysis demonstrated that the males from pupae reared at different temperatures qualitatively released the same mixture of compounds, mainly (*E*,*E*)-α-farnesene, (*Z*,*E*)-α-farnesene and (*Z*)-3-nonenol, previously identified by Heath *et al.* (2000), Ibáñez-López & Cruz-López (2001) and an unidentified compound also described by López-Guillén (2008). However, the released compounds (*E*,*E*)-α-farnesene, the unknown compound and (*Z*)-3-nonenol varied quantitatively with temperature (F = 76.91; df = 3, 908; $P < 0.05$). The amounts of (*Z*,*E*)-α-farnesene emitted were not significantly different among temperatures (F = 0.83; df = 3, 59; $P > 0.05$) (fig. 3).

Effect of temperature on sexual competition

During sexual competition, it was noted that the number of wild male matings was significantly greater than that of the mass-reared males (F = 13.69; df = 4, 25; $P < 0.05$) (fig. 4). However, among mass-reared flies, males from pupae developed at 18°C and 20°C recorded the largest number of matings (F = 13.69; df = 4, 25; $P > 0.05$), and males from pupae developed at 30°C recorded the lowest number of matings (F = 13.69; df = 4, 25; $P < 0.05$).

Effect of temperature on fecundity and fertility

The largest numbers of eggs were produced by females from pupae developed at 18°C and the lowest quantity by females from pupae developed at 30°C. At temperatures of 20°C and 25°C no significant differences were found (F = 1.74; df = 3, 36; $P > 0.05$) (table 3). Regarding fertility, no significant differences were found among females from pupae reared at different temperatures (F = 0.78; df = 3, 36; $P > 0.05$) (table 3).

Table 3. Fecundity and fertility of *A. obliqua* females from pupae that developed at different temperatures.

Temperature (°C)	Fecundity (eggs per female per day ± SE)	Fertility (% hatching ± SE)
18	14.90 ± 2.34 a	84.71 ± 1.78 a
20	11.43 ± 1.83 ab	86.50 ± 1.94 a
25	11.38 ± 1.27 ab	84.14 ± 1.76 a
30	09.87 ± 0.99 b	82.63 ± 1.75 a

Different letters within columns (a, b, c) indicate significant differences ($P < 0.05$).

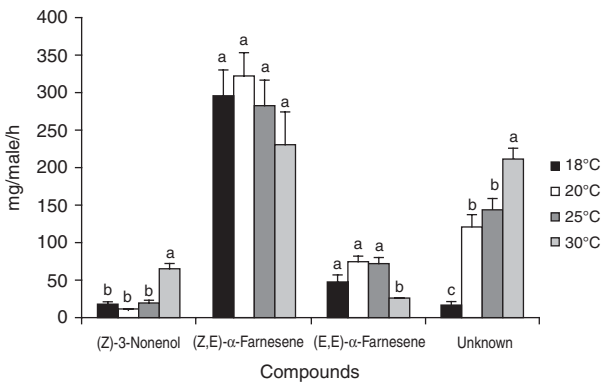

Fig. 3. Amount of volatiles emitted by 8-day-old *A.obliqua* males from pupae reared at different temperatures.

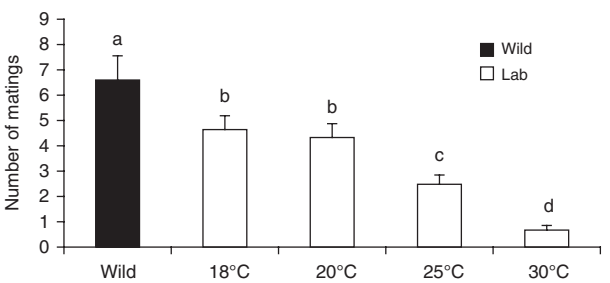

Fig. 4. Sexual competition between *A. obliqua* males exposed to different temperatures in their pupal stage and wild insects. Different letters above bars indicate significant differences ($P < 0.05$).

Discussion

The influence of temperature during development and its effect on biological phase and quality of *A. obliqua* adults were studied. The lower pupation and greater weight loss of larvae exposed to 18°C could be attributed to increased dehydration caused by a longer development period. As expected, temperature showed a significant effect on pupal development time. These results were similar to those found in *Ceratitis capitata* (Wied.), where temperature was directly related to the

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development of the pupal phase (Crovetti *et al*., 1986). In the case of flyers, it has been reported that both radiation and storage temperature lead to a reduction of flight ability (Toledo *et al*., 2004; Resilva *et al*., 2007). Our results show a similar tendency since the lowest percentages of flyers were recorded in adults from pupae that were developed at 18°C and 20°C.

Sexual activity in *A. obliqua* has been evaluated in relation to various parameters such as age, time of day, effect of irradiation and host presence (Aluja & Birke, 1993; López-Guillén *et al*., 2008). However, there were no studies on how temperature conditions during pupal development affect their sexual performance. We found that low temperatures during development (18°C and 20°C) gave rise to males with greater calling and mating propensity. This could be explained as a result of the relaxed development of the sexual organs at low temperatures allowing more time for a homogeneous maturation (Fletcher, 1989; Taufer *et al*., 2000). Another explication could be that at higher temperatures the crowded conditions produce metabolic heat, which could have a detrimental effect on the sexual behavior of the adults. A third reason could be heterogeneity selection, where higher mortality at the pupal stage produces more robust and competitive adults at the lower temperatures.

The amounts of (*Z*,*E*)-α-farnesene released by males from pupae developed at the four temperatures did not show significant differences. However, more (*E*,*E*)-α-farnesene was produced at temperatures of 18°C, 20°C and 25°C than at 30°C. Males originating from pupae exposed to 30°C displayed higher production of the unidentified compound and (*Z*)-3-nonenol, compared with males from other temperatures. It is possible that increased production of this compound by males at 30°C affected attraction by wild females, since it is known that, if volatile compound concentration varies, behavioral responses could be different (McNeil, 1991). In the sexual competition experiment, males from pupae which developed at 30°C recorded the lowest number of matings. In males from pupae that developed at 25°C, the amount of volatile emitted decreased after reaching ten days of age but showed slight recovery at 14 days; a similar trend was observed by López-Guillén (2008). This suggests that accelerated development at temperatures of up to 30°C had an adverse effect on the insects' sexual maturity, resulting in a change in volatile production. Possibly, heat stress caused deficient development of their sexual organs (Fletcher, 1989; Taufer *et al*., 2000). Our results show that *A. obliqua* male calling behavior started in all treatments at six days of age when the number of males calling was lower than at 8, 10 and 12 days old. López-Guillén *et al*. (2008) point out that the emission of volatiles is significantly affected by age in *A. obliqua* males.

Regarding female fertility, we found no significant differences among temperature treatments. However, females from pupae that developed at lower temperatures showed the highest level of fecundity. The 17-day-old difference in development time between the highest and lowest temperatures could explain the difference in egg production. Longer developmental time resulted in greater capacity for egg production. But, when pupa development was at 25°C, it resulted in a shorter development period (13 days), a reduction in weight loss, a high percentage of pupation, emergence and flyers, and an increase in egg production. All these attributes are ideal for rearing purposes.

In conclusion, in this study, we found a marked effect of pupal development temperature on pupa development time, adult emergence, sexual maturity, mating competitiveness and female fecundity of *A. obliqua* flies. It appears that the main advantage for keeping pupae at 25°C, instead of 18°C or 20°C, is the drastic reduction in pupal developmental time, which is important in reducing infections and rearing costs. In addition, this temperature favors adult emergence and flying ability. In contrast, pupa weight and mating competitiveness were significantly favored when pupae developed at 18°C and 20°C. Based on these results, an environmental temperature of 25°C during pupal developmental time is recommended for *A. obliqua* mass-rearing.

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