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Effects of different temperature regimens on the development of *Aedes aegypti* (L.) (Diptera: Culicidae) mosquitoes

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ABSTRACT

This study was conducted to determine the effects of increased water temperatures on the development of *Aedes aegypti* immatures under laboratory conditions in Trinidad, West Indies using temperature regulated water baths to cover a range of temperatures from 24–25 °C to 34–35 °C at a relative humidity of 80%. Two experiments were designed: (1) at constant temperature regimens and (2) under diurnal temperature regimens ranging from 24–25 °C to 34–35 °C. At 24–25 °C egg hatching success was 98% at 48 h, however at 34–35 °C egg hatching rates declined to 1.6% after 48 h. *Ae. aegypti* larvae reared under constant temperature regimens showed pupation on day 4 with highest pupation occurring at 30 °C (78.4%) However, under diurnal temperature regimens, pupation began on day 4 but only at the higher temperatures of 30–35 °C. Under diurnal temperature regimens ranging from 24 °C to 35 °C significantly more females emerged at higher temperatures, than males. In contrast, at constant temperatures of 24–35 °C no significant difference in M/F ratios were observed. The body size of *Ae. aegypti* reared at constant temperature regimens was significantly larger than males and females larvae reared under diurnal temperature regimens of 25–30 °C. The results of this study are discussed in the context of changing or increasing water temperatures, seasonal changes in vector populations and vector competence. Using these key factors control strategies are recommended to manage vector populations as expected increases in temperatures impact the Caribbean region.

1. Introduction

Advances in the science of climate change and in the epidemiology of dengue fever (DF) have demonstrated marked changes in disease transmission patterns (Gubler and Kuno, 1997; Guha-Sapir et al., 2005; Chadee et al., 2007) and changes in the behaviour and ecology of the dengue vector, *Aedes aegypti* (L.) mosquitoes (Chadee and Martinez, 2000; Chen et al., 2006; Hemme et al., 2010). Within the Caribbean and Latin American region outbreaks of dengue fever and its hemorrhagic manifestations were known to occur in cycles, occurring every 5–10 years (Gubler and Kuno, 1997) but recent changes in the epidemiology of the disease have resulted in an inc rease in the frequency of outbreaks.

The mosquito vector *Ae. aegypti* is known to be able to adapt to varying environmental conditions, as it is poikilothermic and has shown seasonal increases in the vector population and seasonal variability in vector competence (Paupy et al., 2003). Multiple anthropogenic and biological factors have been attributed to the changing epidemiology of DF and ecology and behaviour of the vector: including demographic changes in the human populations (Gubler and Kuno, 1997; Chadee, 2004), urbanization (Chadee, 2010), speed and volume of international traffic (Gubler and Kuno, 1997; Chadee and Martinez, 2000), introduction of new dengue genotypes (Rico-Hesse, 1990), failure of vector control programs due to insecticide resistance (Rawlins, 1998; Polson et al., 2011), poor management practice (Rosenbaum et al., 1995; Chadee et al., 2004) and seasonal peaks in the vector population and in dengue occurrence (Chen et al., 2006; Chadee et al., 2007).

Recent studies on climate variability and climate change forecast a global increase in temperatures of 1.4–5.8 °C (IPCC, 2007) and these changes can impact development times and the vectorial capacity of the *Ae. aegypti* mosquito. The speed and duration of larval development is governed by a series of internal and external factors (Christophers, 1960; Clements, 1999) but one of the most important external drivers is temperature. Some studies have shown that the age at pupation and adult size of various mosquito species may reflect the environmental conditions during growth of the larval stages (Reisen et al., 1984; Fish, 1985; Haramis, 1985; Lyimo et al., 1992). Laboratory studies have also shown that larvae reared at high temperatures and under food stress conditions develop into small adults and experience high mortality (Reisen et al., 1984; Siddiqui et al., 1976). Conversely, larvae reared at high temperatures and fed optimally developed into large adults (Tun-Lin et al., 2000). Kamimura et al. (2002) reported that larval

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rearing temperatures can have a major impact on disease transmission by affecting body size, development time and production. It is therefore important to conduct studies on the impact of different temperatures on the duration of the immature stages of *Ae. aegypti* in order to explain the finding from previous studies some of which included confounding factors like differential food supply and crowding of rearing containers (Southwood et al., 1972) and to be able to forecast impacts of future climate change events on the mosquito populations. This study examines the effects of different temperatures on the development of *Ae. aegypti* and their impact on adult emergence under laboratory conditions.

2. Materials and methods

2.1. Mosquitoes

The *Ae. aegypti* mosquitoes used in this study were obtained as eggs using modified ovitraps (Fay and Eliason, 1966) in the field in Curepe (10°38′N; 60°24′W), Trinidad, West Indies. Eggs collected were examined under a microscope (at 40×) for the chorionic pattern which is reported to be characteristic of *Ae. aegypti* (Pratt and Kidwell, 1969). These eggs were identified in the Parasitology Laboratory, Department of Life Sciences, University of the West Indies, St. Augustine, Trinidad. All mosquito eggs collected from the field in Curepe were identified as *Ae. aegypti.*

The duration of immature development times of *Ae. aegypti* was assessed under: (1) constant temperature regimens and (2) under a diurnal temperature regimen, for a range of temperatures from 25 to 35 °C at 80% relative humidity.

2.2. Egg hatching experiment

Temperature regulated water baths were set up to cover a range of temperature; 24–25 °C, 26–27 °C, 29–30 °C, 32–33 °C and 34–35 °C. Six replicate 250 mL beakers containing 150 mL of water was placed in each bath and allowed to acclimatize for 24 h. A paper strip containing 30–40 eggs collected from the field was placed in each beaker and allowed to incubate and hatch for 24 h. At the end of this period, the number of eggs hatched was counted and the remaining eggs on the strips allowed to hatch for a further 24 h, after which the number of eggs hatched was again determined. The percentage of eggs hatched after 24 and 48 h was determined for each temperature treatment.

2.3. Effects of constant temperatures on larval and pupal development

Temperature regulated water baths were set up to capture the range of temperature 24–25 °C, 26–27 °C, 29–30 °C, 32–33 °C and 34–35 °C. At each temperature 6–8 1 L beakers containing 800 mL of water were allowed to acclimatize for 24 h. Circa 100 newly hatched *Ae. aegypti* larvae were placed in each beaker and fed daily with 0.1 g of ground fish food. Pupae were removed on a daily basis, and placed in individual chambers until the adults emerged. The rate of pupation was calculated for each treatment temperature, based on the total number of pupae obtained at the end of the development period. The number of adult males and females emerging was enumerated and used to determine the male/female (M/F) ratio for emergent adults for each treatment temperature. The wings of both males and females were dissected out and mounted on glass slides in a drop of saline solution. Using a dissecting microscope with an ocular micrometer wing lengths (Fig. 1) were measured from the apical notch to the axillary margin, excluding the wing fringe for each mounted wing as measured by Nasci (1986) and Schneider et al. (2011).

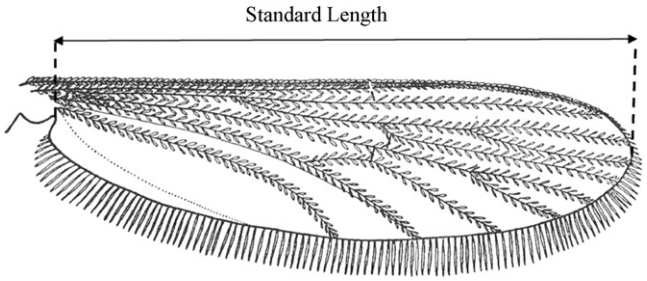

Fig. 1. Diagram showing the standard length measurement for a wing of *Ae. aegypti*.

2.4. Effects of diurnal temperatures on larval and pupal development

This experiment was repeated with the water baths turned on at 8 am and off at 5 pm, thus gradually heating up to the designated maximum temperature level set and turned off at 5 pm to allow the water to cool to room temperature (24–25 °C). This approach mimicked the diurnal heating and cooling cycle often observed in the field and was conducted during this study for a range of temperatures; ambient or 24–25 °C, 26–27 °C, 29–30 °C, 32–33 °C and 34–35 °C. These heating and cooling cycles closely coincided with temperatures observed in the field (see Fig. 2) similar to those reported by Hemme et al. (2009).

2.5. Data analysis

Wing-length measurements collected for each temperature treatment were analysed using an ANOVA and Tukey HSD analysis (SYSTAT Ver.5.0) to determine whether any significant differences occurred between and among different temperatures and at different temperature regimens. In addition, hatching rates, rates of pupation and sex ratio data were transformed and converted into contingency tables and subjected to a *G*-test (Petrie and Sabin, 2000) to determine whether any significant differences were observed among the various treatments.

3. Results

3.1. Egg hatching

The percentages of eggs which hatched following submergence in water heated at different temperatures are shown in Fig. 2. At 24–25 °C hatching success was 95% after 24 h and 98% at 48 h. This was significantly ($P < 0.05$) higher than the hatching success at 26–27 °C (37% – 24 h; 57% – 48 h); 29–30 °C (10%, 24 h; 20% – 48 h): 32–33 °C (3.7% – 24 h; 3.7% – 48 h) and 34–35 °C (1.6%, 24 h; 1.6%, 48 h) as shown in Fig. 3.

3.2. Rearing at constant temperature regimens

Ae. aegypti larvae reared under the constant temperature regimens showed greater than 90% survival across all test temperatures. Pupation generally started on day 4, with the highest pupation rate occurring at 30 °C (78.4%) and the lowest at 25 °C (0.5%) (Table 1). This pattern continued until days 7 and 8, resulting in 80–99% pupation across the different temperature regimens (Table 1 and Fig. 4).

The length of the *Ae. aegypti* pupal stage showed no significant difference between temperatures 25–33 °C, however at 35 °C, pupation was only 80%, significantly ($P < 0.05$) less than those of the other temperatures (Fig. 4). Adults emerged within 2–3 days and the ratio of males/females (M/F) generally ranged from 0.9 at 30 °C to 1.16 at 27 °C and 35 °C (Fig. 5A). There was no significant dif-

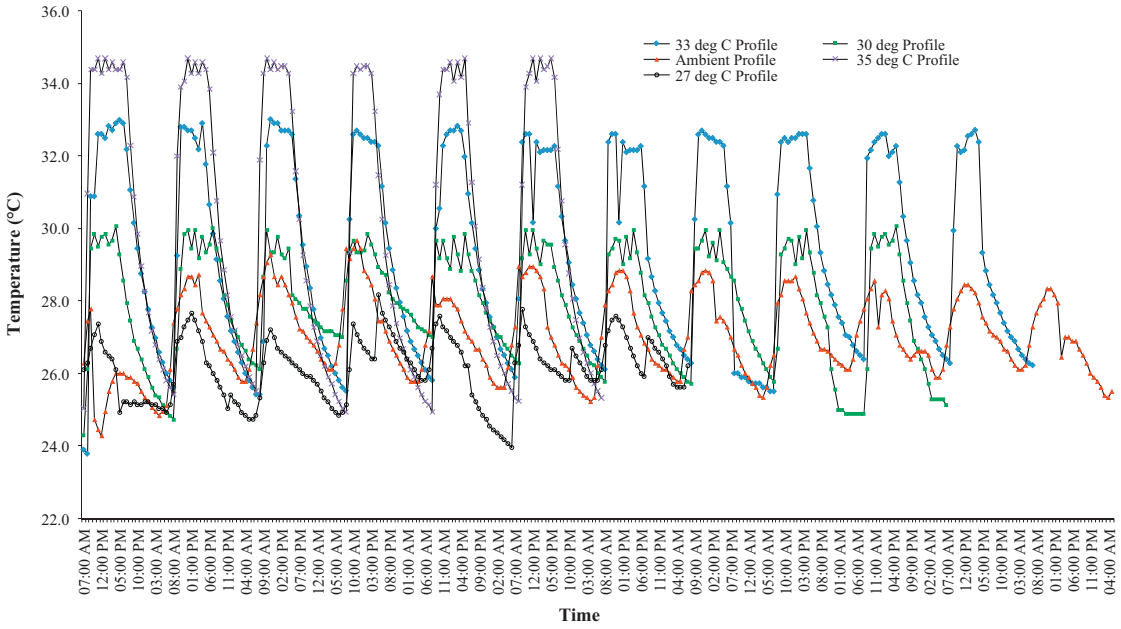

Fig. 2. Temperature profile for *Ae. aegypti* reared on heat cycle at different temperatures (27–35 °C).

Table 1
Cumulative percentage pupation for larvae reared at different temperature for both the constant temperature and cyclic temperature experiments.

Temperature (°C)	Days								
	4	5	6	7	8	9	10	11	12
	Cumulative % pupation under constant temperature								
25	0.5	29.8	76.8	87.7	94.1				
27	39.6	84.8	98	98.5					
30	78.4	92.2	95.6	97.2					
33	14.1	63.5	79.4	87.4	91.8				
35	18.8	34.8	60.8	74.2	79.8				
	Cumulative % pupation under diurnal temperature								
Ambient			6.3	26.6	37	57.3	73	82.5	87.8
26–27		9.4	51.6	70.2	78.9				
29–30	2.0	24.1	51	68.3	75.9	82.2	86		
32–33	5.0	19.5	41.5	79.1	83.2	86.4	89.2		
34–35	23.5	40.3	60.7	68.6	86				

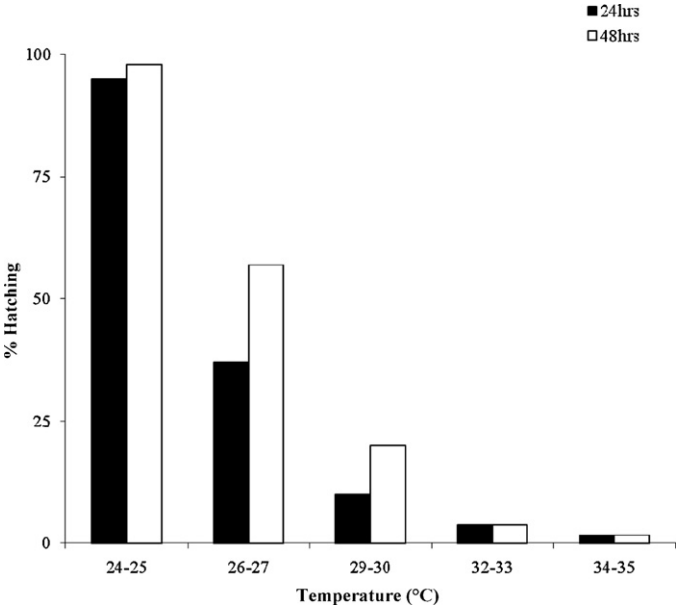

Fig. 3. The percentage of *Ae. aegypti* eggs hatched at different temperatures (25–35 °C).

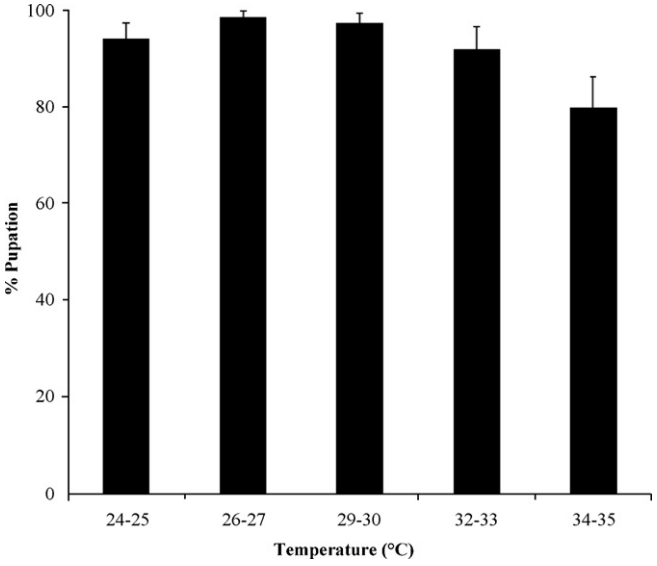

Fig. 4. Average percentage pupation of *Ae. aegypti* maintained at different temperatures (2535 °C).

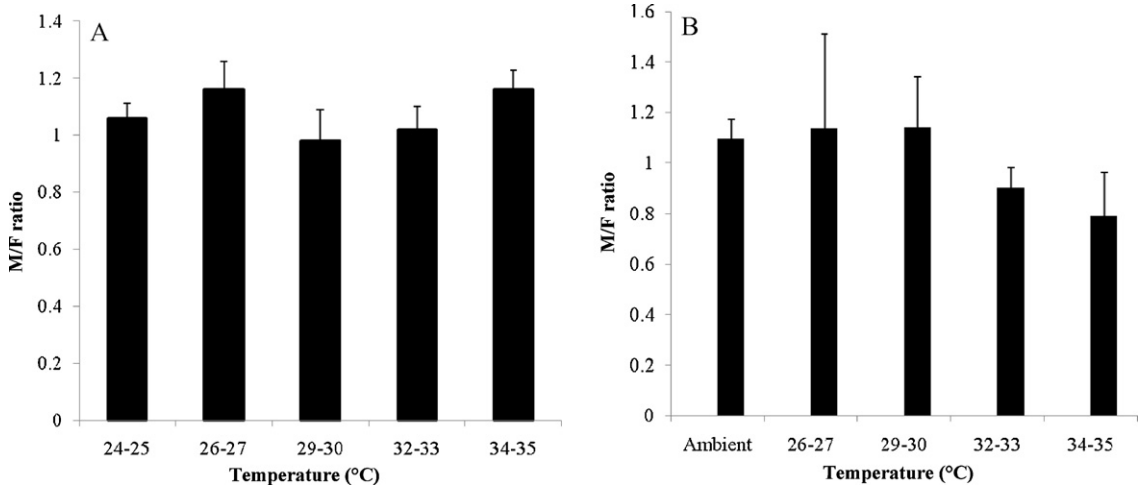

Fig. 5. Ratio of male to female *Ae. aegypti* adults that emerge after larvae were maintained at (A) constant temperatures (25–35 °C) and (B) after an 8 h heating cycle at different temperatures (24–35 °C).

ference in the M/F ratio from larvae kept at constant temperature from 25 °C to 35 °C (Fig. 6A).

Males obtained from larvae maintained at the constant temperature regimens, showed a significant decrease in wing length with increasing temperature (Fig. 6A). Development at 33 °C and 35 °C produced males (2 mm) with significantly smaller ($P < 0.05$) wings than those developed at 25–30 °C (2.17 – 2.27 mm). Females also showed a significant ($P < 0.05$) decrease in average wing length with increasing temperatures. Development at 33 °C and 35 °C produced females with significantly smaller wings (2.5 mm) than those developed at 25–30 °C (2.82–2.98 mm).

3.3. Rearing at diurnal temperature regimens

Ae. aegypti larvae reared under conditions simulating the diurnal temperature cycle (daily heating and cooling) is shown in Fig. 2. The duration of the peak in each exposure temperature reflected the pattern recorded for ambient conditions (Fig. 5B). Under the diurnal temperature regimens, pupation began at day 4 but only at the higher temperatures (30–35 °C). At 24–25 °C, pupation started on day 6 and ended on day 12 (Table 1). Pupation varied between 79 and 90% for each of the temperature regimens under the diurnal cycle, with no significant differences being observed between the percentage pupation, at the end of the pupal stage (Fig. 7).

However, larvae maintained on a diurnal cycle at temperatures between ambient or 24 °C and 35 °C, showed significantly more females emerging at the higher temperatures (Fig. 5B). Larvae reared at 33 °C and 35 °C produced M/F ratios of 0.9 and 0.79, respectively, which was significantly lower than the M/F ratios at the lower temperatures (M/F = 1.1–1.14). The M/F ratio typically shows a dominance of males from pupae obtained within 2–3 days of the start of pupation. However, pupae were obtained for six days after the start of pupation, with predominately females being observed after 3 days.

Larvae reared under the diurnal temperature cycle also produced significantly larger females than males, as expected (Fig. 6B). However there was no significant difference in the wing lengths for either the males or the females across the different test temperatures. Males showed only a small positive correlation between wing length and temperature (0.16) while females showed a small negative correlation (−0.34).

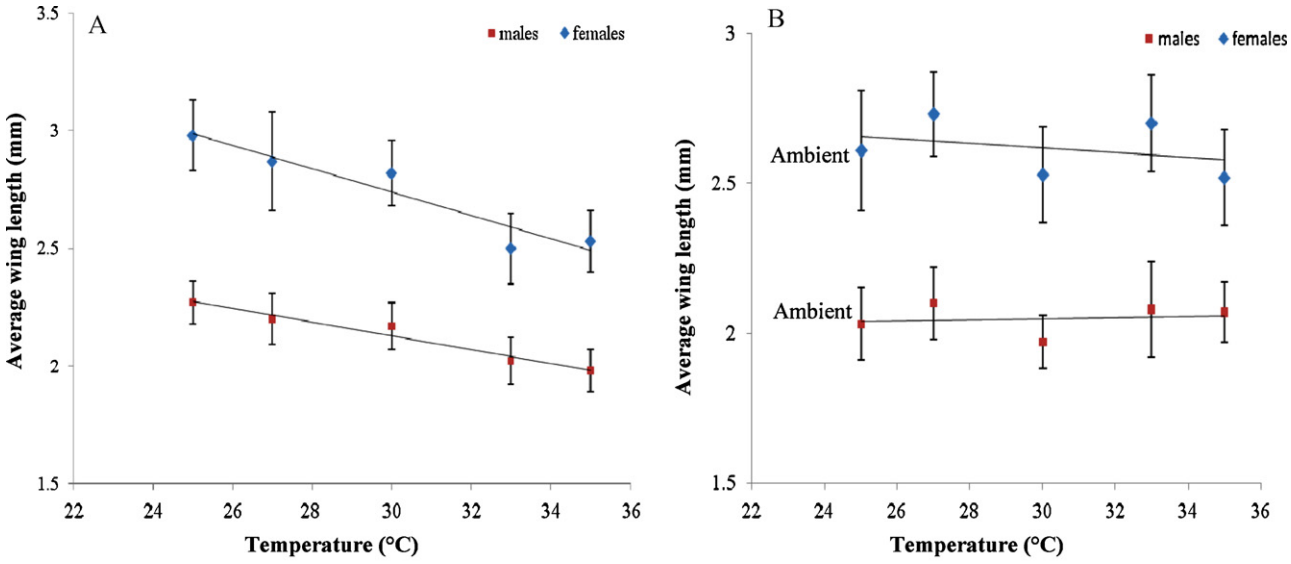

Fig. 6. Average wing lengths of male and female *Ae. aegypti* adults that emerge after larvae were maintained at (A) constant temperatures (25–35 °C) and (B) after an 8 h heating cycle at different temperatures (24–35 °C).

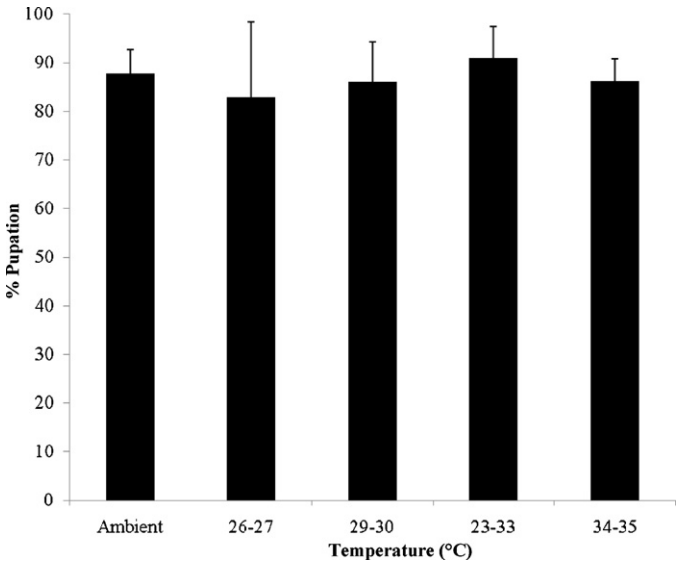

Fig. 7. Average percentage pupation of *Ae. aegypti* from larvae maintained on a diurnal temperature cycle for temperatures (25–35 °C).

4. Discussion

In tropical countries, the current projection for increases in temperatures using climate change scenarios (models) suggests that average daily temperatures of 29 °C may in the future increase to between 30.4 °C and 34.8 °C (IPCC, 2007). These increases in temperature may have a significant impact on the biology of *Ae. aegypti* mosquitoes (Bar-Zeev, 1958; Tun-Lin et al., 2000) and their vector competence (Morales Vargas et al., 2010; Schneider et al., 2011). *Ae. aegypti* egg hatching is usually stimulated by three factors: ambient oxygen concentration in the water (Gjullin et al., 1941), conditioning of eggs at room temperatures of 26.6–27.0 °C and a relative humidity of 50–80% (Mulla and Chaudhury, 1968). The present results showed a hatching rate of over 95% after 48 h at 24–25 °C and 80% relative humidity but the rate significantly ($G = 23.7$; d.f. 5; $P < 0.001$) declined as temperatures increased from 29 °C to 35 °C. These results suggest that as temperatures increase (due to the force of climate change), egg hatching rates may decline and may eventually lead to a decline in the *Ae. aegypti* populations during both wet and dry seasons (Chadee et al., 2007). The low hatch rate recorded at 35 °C (1.6%) is consistent with the results reported by Mulla and Chaudhury (1968) who also reported that a temperature of 37 °C was lethal to *Ae. aegypti* eggs.

In a recent study, Hemme et al. (2009) reported the absence of *Ae. aegypti* immatures in containers, in which water temperatures exceeded 32 °C. The daily temperature profile in water drums (see Hemme et al., 2009, Fig. 2), the primary breeding sites of these mosquitoes in Trinidad and Tobago (Chadee and Rahaman, 2000; Chadee, 2003) suggest that eggs may fail to hatch in Trinidad because water temperature exceeds 32–35 °C. It should be noted that although laboratory (present study) and field studies (Bond and Fay, 1969; Hemme et al., 2009) suggest the absence of *Ae. aegypti* immatures in water containers which exceeded 32 °C, most breeding sites are found in shaded environments where water temperatures may not exceed 32 °C and thus may not affect egg hatching *per se*. In fact these results suggest that as temperatures increase the *Ae. aegypti* may well return to feral or natural breeding habitats which are usually located in peridomestic or cooler environments. For example, Kellett and Omardeen (1957) and McClelland (1967) reported an apparent shift in the breeding behaviour of *Ae. aegypti* from artificial containers to tree-holes during an *Ae. aegypti* eradication program in Trinidad and attributed this to the application of BHC at oviposition sites.

In tropical countries, the duration of larval and pupal developmental times of *Ae. aegypti* have been found to vary with respect to temperature (Bar-Zeev, 1958; Christophers, 1960; Rueda et al., 1990), food supply (Christophers, 1960; Tun-Lin et al., 2000) and density or crowding of breeding sites (Mulla, 1979). During the present study the immatures were fed optimally and care was taken to prevent over crowding so, therefore, the results reported here represent the effects of temperatures ranging from 24 °C to 35 °C on the development of the immature stages of the *Ae. aegypti* mosquitoes. The decrease in wing lengths for both males and females showed a strong negative correlation with temperature (−0.98 males; −0.95 females) suggesting a direct relationship between temperature and size of adults, that is, higher temperatures produce significantly ($P < 0.05$) smaller adults. The shorter development time at the higher temperatures generally resulted in significantly ($P < 0.05$) smaller adults (Fig. 6A and B). Similar results have been reported (Bar-Zeev, 1958; Tun-Lin et al., 2000) with larger females collected at lower temperatures, e.g. 3.4 mm wing length at 15 °C vs 1.8 mm wing length at 35 °C (Tun-Lin et al., 2000).

The development time for *Ae. aegypti* reared under the diurnal temperature regimen was 7–10 days at 25 °C and 7–9 days at 30 °C, which was consistent with the results by Kamimura et al., 2002 and Tun-Lin et al., 2000. However, at 35 °C the development time (from first instar to adult stage) was 6–7 days showing that as temperatures increase, the mosquito development time is reduced but contrary to the situation with constant temperature rearing regimens the size of the mosquitoes is unaffected. These results are different from those previously reported (Tun-Lin et al., 2000; Mourya et al., 2004) possibly because those studies were conducted using different geographic strains and using constant water temperatures throughout the study period while the present study was conducted using two distinctly different temperature regimens and the Trinidad strain of *Ae. aegypti* mosquitoes. The results showed that there were distinct differences in developmental times (Table 1) and in size of *Ae. aegypti* (Fig. 6A and B) between mosquitoes reared at constant temperatures vs diurnal temperature regimens.

An important finding of this study was the modification in the male/female sex ratios, with larvae reared at 33 °C and 35 °C producing M/F ratios of 0.9 and 0.79, respectively, which was significantly lower than the M/F ratios found at the lower temperatures (M/F = 1.1–1.14). The M/F ratio typically shows a dominance of males from pupae obtained within 2–3 days, post pupation but the present results revealed that adults emerging from pupae after day 6 were predominately females. Similar results were previously found by normal and temperature tolerant strains in India, with more females being produced among both strains at high temperatures (28 °C and 37 °C) (Mourya et al., 2004). Since, the sex ratios of mosquitoes are modulated by genetic mechanisms further studies are recommended because studies conducted by Cha et al. (2006) demonstrated the presence of a meiotic driver with relatively high frequencies of driver males and varying degrees of responder sensitivities in Trinidad.

The body size of the *Ae. aegypti* mosquitoes has been suggested to indicate their ability to adapt to changing extreme conditions in the environment. There is evidence to support seasonal variability in vector competence for DF in *Ae. aegypti* in Cambodia (Paupy et al., 2003) and smaller size females occurring during the dry season in Thailand (Morales Vargas et al., 2010). It is noteworthy that the present results suggest that even though daily mean temperatures may increase, it may not have an effect on the size of adults because of the presence of the cooling phase. In Trinidad, there is usually a difference of 10 °C between daytime

and night time maximum and minimum temperatures (Chadee et al., 2007) with cooling and heating phases observed in water containers by Hemme et al. (2009) and simulated during the present study. The males and females produced from larvae maintained at a constant temperature were significantly larger than males and females from larvae maintained on the diurnal temperatures ranging from 25 to 30 °C. However, at the higher temperatures (33–35 °C) mosquitoes reared under the diurnal temperature cycle were larger than those reared under constant temperature. These results suggest that as the climate changes and extremes in temperatures are found, *Ae. aegypti* mosquitoes may well become efficient potential vectors with increasing body size, ability to adapt to higher temperature ranges which may shorten extrinsic incubation periods for arboviruses. Based on these results vector control programs should plan intervention strategies based on changing container profiles (e.g., key containers), seasonal extremes in local or regional weather conditions and introduce integrated vector management approaches.

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