Impact of small variations in temperature and humidity on the reproductive activity and survival of *Aedes aegypti* (Diptera, Culicidae)

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ABSTRACT. Impact of small variations in temperature and humidity on the reproductive activity and survival of *Aedes aegypti* (Diptera, Culicidae). In short space of time increase in temperature and rainfall can affect vector populations and, consequently, the diseases for them transmitted. The present study analyzed the effect of small temperature and humidity variations on the fecundity, fertility and survival of *Aedes aegypti*. These parameters were analyzed using individual females at temperatures ranging from 23 to 27 °C (mean 25 °C); 28 to 32 °C (mean 30 °C) and 33 to 37 °C (mean 35 ºC) associated to 60±8% and 80±6% relative humidity. Females responded to an increase in temperature by reducing egg production, oviposition time and changing oviposition patterns. At 25 ºC and 80% relative humidity, females survived two-fold more and produced 40% more eggs when compared to those kept at 35 ºC and 80% relative humidity. However, in 45% of females kept at 35 ºC and 60% relative humidity oviposition was inhibited and only 15% females laid more than 100 eggs, suggesting that the intensity of the temperature effect was influenced by humidity. Gradual reductions in egg fertility at 60% relative humidity were observed with the increase in temperature, although such effect was not found in the 80% relative humidity at 25 º C and 30 º C. These results suggest that the reduction in population densities recorded in tropical areas during seasons when temperatures reach over 35 ºC is likely to be strongly influenced by temperature and humidity, with a negative effect on several aspects of mosquito biology.

KEYWORDS. Climate changes; dengue; fecundity; fertility; mosquito.

RESUMO. Impacto de pequenas variações de temperatura e umidade na atividade reprodutiva e sobrevivência de *Aedes aegypti* (Diptera, Culicidae). Em curto espaço de tempo, um aumento na temperatura e precipitação pode afetar a população de vetores e conseqüentemente, as doenças por eles transmitidas. Nesse estudo, analisou-se o efeito de pequenas variações na temperatura e umidade, sobre fecundidade, fertilidade e sobrevivência de *Aedes aegypti*. Esses parâmetros foram investigados usando-se fêmeas individuais nas temperaturas: 23-27 ° C (média 25 ° C), 28-32 ° C (média 30 ° C) e 33-37 ° C (média 35 º C) associada à umidade relativa: 60 ± 8% e 80 ± 6%. As fêmeas responderam ao aumento da temperatura com redução na produção de ovos, tempo de oviposição e mudança nos padrões de postura. A 25 º C e 80%, fêmeas sobreviveram duas vezes mais e produziram 40% mais ovos, que aquelas mantidas a 35 º C e 80%. No entanto, nos grupos a 35 º C e 60% a postura foi inibida em 45% das fêmeas e apenas 15% puseram mais de 100 ovos, sugerindo que a intensidade do efeito da temperatura seja influenciado pela umidade. Reduções graduais na fertilidade a 60% de umidade relativa foram observadas com o aumento da temperatura, embora esse efeito não tenha sido registrado na umidade de 80%, nas temperaturas de 25 º C e 30 º C. Esses resultados sugerem que a redução na densidade populacional nas zonas tropicais durante estações, em que a temperatura se eleva acima de 35 º C pode ser fortemente influenciada pela interação temperatura e umidade, afetando negativamente diversos aspectos da biologia do mosquito.

PALAVRAS-CHAVE. Mudanças climáticas; dengue; fecundidade; fertilidade; mosquito.

One of the most important mosquito-borne diseases affected by climate changes is dengue fever (DF), which continues to spread throughout tropical and subtropical regions worldwide, affecting an estimated 50–100 million people each year, except Europe (WHO 1997).

The greatest effect of climate change, which is expected to raise temperatures an average of 1.0 to 3.5 ºC by the year 2100 (Houghton *et al.* 1996), is likely to be observed in transmission areas with an extreme temperature range (Githeko *et al.* 2000). The variability in temperature, precipitation and humidity expected to take place under different climate changes will affect the biology (Chadee 1992; Kalra *et al.* 1997; Teng & Apperson 2000) and ecology (Alto & Juliano 2001; Miciele & Campos 2003; Vezzani *et al.* 2004) of mosquito vectors and intermediate hosts as well as the risk of disease transmission (Moore *et al.* 1978).

The main vector of dengue fever is the mosquito *Aedes aegypti* (Linnaeus, 1762) originally from northeastern Africa and having spread to other parts of the world, especially tropical and subtropical regions (Gubler 2002). The wide geographic distribution of *A. aegypti* is likely to be associated with variations in its biology (Glasser & Gomes 2002; Beserra *et al.* 2006), enabling it to survive in a variety of different environmental conditions. This mosquito species show breeding preferences for domestic water containers having its proliferation influenced by human population growth, general travel, lack of political will, limited financial and human resources to implement effective control measures (WHO 2002).

Studies aiming to understand the effect of temperature on mosquito population dynamics generally investigate variations between 20 and 30 °C (Joshi 1996; Löwenberg-Neto & Navarro-Silva 2004). However, in tropical areas in which *A. aegypti* is a vector of etiological agents causing

dengue and yellow fever, mean temperatures are generally high and can rise above 35 °C. Therefore, detailed studies on the effect of abiotic factors on mosquito reproduction under controlled laboratory conditions can contribute to a more precise field data interpretation. A large genetic variation is observed in *A. aegypti* result in different physiological, bionomic and behavioural aspects amongst close related mosquito population (Ayres *et al.* 2004). For instance, changes in the duration of the *A. aegypti* lifecycle that have been described between populations in nearby cities as a result of temperature variations are likely to be associated to mosquito adaptation to local climatic changes (Beserra *et al.* 2006). Therefore, control strategies depend upon an understanding of local mosquito populacion dinamic would result in practical regional strategies, especially regarding the improvement of vector control programs, such as to indicate the best moment for measure control.

Recife is a coastal city in northeastern Brazil, with temperatures ranging from 22º C to 32º C and relative air humidity between 70% and 90% throughout the year, being a factor that favour mosquito breeding all year round (Regis *et al.* 2008). Taking into account the predicted temperature increase due to global warming, the aim of the present study was to assess the impact of a small rise in temperature on the reproductive fitness and survival of *A. aegypti* females, originally from the Recife mosquito population. The results broaden knowledge on the biology of this vector, thereby offering support for the improvement of control measures regarding this mosquito species in the area.

MATERIAL AND METHODS

Mosquitoes. *Aedes aegypti* females from a laboratory colony, originally formed from eggs collected in ovitraps placed in an urban area of Recife (Lat 08°04'S Long 34°52'W), Brazil, were used as biological material in this study. The city of Recife has two seasons (rainy and dry), with maximal temperatures reaching over 35ºC in the dry season. For colony maintenance, larvae were routinely reared in plastic containers (40 x 27 x 7,5 cm) with tap water and fed with commercial cat food (0.04 mg/larva) under laboratory conditions (27±2 °C; 70±5% relative humidity and a photoperiod of 12:12 L:D) stimated using a using a thermo-hygrometer (INCOTERM). Adults were maintained with a 10% sucrose solution and females were fed on mice in order to stimulate egg production.

Effect of the temperature and humidity on fecundity and survival. Fecundity was estimated based on the number of eggs laid by females in the first gonotrophic cycle, which, according to Suleman (1990), is a prognosis of total fecundity.

Six experimental groups were performed, using females randomly and individually separated into plastic containers (300 ml) immediately following the blood meal. Four consecutive experiments were carried out, using 20 to 37 female/trial, each female being considered a replicate, in the following conditions: females maintained at temperatures ranging from 23 to 27 °C (mean: 25°C) and relative humidity of 60±8% (n= 113) or 80±6% (n= 105); from 28 to 32 °C (mean: 30 °C) combined with relative humidity of 60±8% (n= 149) or 80±6% (n= 100); from 33 to 37 °C (mean: 35 ºC) and relative humidity of 60±8% (n= 100) or 80±6% (n= 110).

Throughout this paper, mean values are used to refer each experimental setting. Temperature and humidity readings were taken twice daily. Daily oviposition was observed on water-soaked filter paper (9 cm in diameter) inserted in the container as an oviposition substrate. The substrates were left to dry for seven days under the same experimental conditions of their respective groups and were then analyzed under an optical microscope (x10) for the determination of the number of eggs laid. Survival rate was estimated from the number of living individuals in each group during daily observations in females deprived from suggar feeding. Feeding on fructose is relatively rare for wild *A. aegypti*, living in the dwellings of their human hosts and seems do not affect survival and reproductin (Edman *et al.* 1992; Harrington *et al.* 2001).

Influence of temperature and humidity variations on hatching rate. From each setting, a group of eggs was randomly selected for the investigation of hatching rate. The eggs were placed in plastic trays with tap water (2 liters) for larvae hatching. Larvae were counted and fed on cat food (0.04 mg/larva). After pupation, the individuals were collected, placed in plastic containers and placed into cages for adult emergence. Afterwards, the adults were analyzed to determine sexual proportion.

Statistical analysis. Statistical analysis were performed using the BioEstat® 5.0 for Windows. The effects of temperature and humidity on oviposition rate, egg hatching and survival were analyzed with two-way analysis of variance (ANOVA, Tukey *a posteriori* test). Data were previously tested for normality using the Kolmogorov-Smirnov test and when represented by percentages, the data were transformed by the square root of the percentile divided by 100. The influence of abiotic factors on the mean number of eggs laid and survival rate of *A. aegypti* females was estimated using the Student's *t*-test and simple linear regression, respectively.

RESULTS

Fecundity and Survival. The effect of temperature and humidity on fecundity in the first gonotrophic cycle of *A. aegypti* females was investigated in 678 individuals. Both temperature and humidity influenced the number of eggs laid as well as the number of females that laid eggs (Table I). A reduction in oviposition rate was observed with the increase in temperature, whereas the intensity of the reduction was influenced by humidity. The lowest oviposition rate (mean = 54.53 ± 4.81 eggs) was recorded in the group of females kept at the highest temperature and lower humidity (35 ºC and 60% relative humidity). Contrarily, the highest rate (mean = 99.08 ± 3.56 eggs) was obtained at the lowest temperature (25 °C) and higher humidity (80%) (Table I).

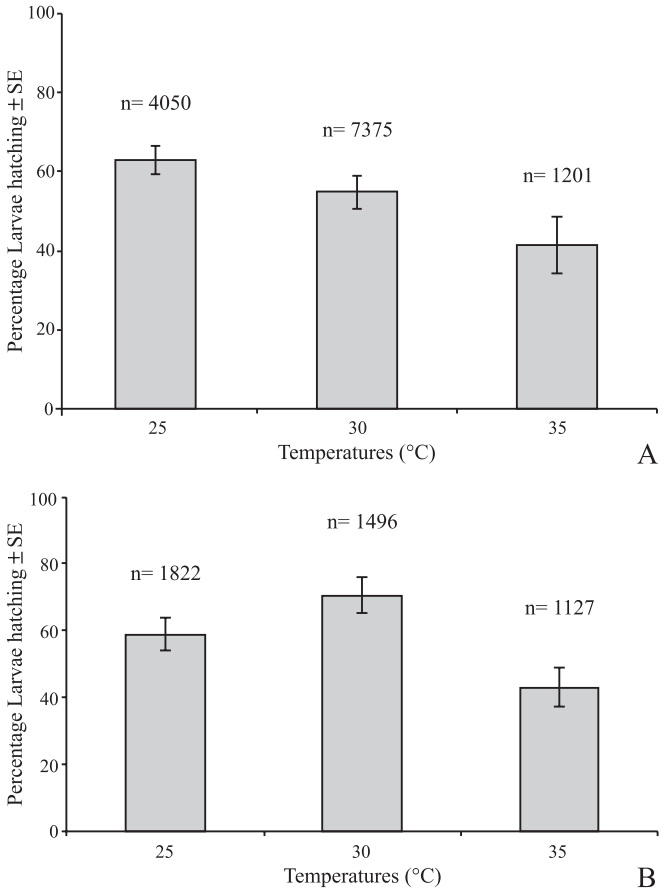

Fig. 1. Fertility rates of eggs maintained under different temperature and humidity. A - 60% rh; B- 80% rh. n = number of eggs analysed.

A significant reduction in number of eggs laid occurred as the temperature increased (F= 25.8198, df = 243, p< 0.01) and the humidity was kept at 80%. Under this condition, a reduction of 23.5% in the mean number of eggs laid by females submitted to 35 °C (mean= 75.75±5.03) was observed in comparison to those maintained at 25 °C. This decrease was more evident (approximately 40%) when the base temperature (25 ºC) was increased by 10 ºC (Table 1). The effect of temperature on egg production was less evident in females maintained at the lower humidity (60%). At this humidity setting, a significant reduction was only recorded in the group kept at 35 ºC in comparison to the other temperatures tested (F= 170.418, df = 265, p< 0.01). Although females kept at 30 ºC laid fewer eggs on average than at 25 ºC (Table 1), the differences between groups did not achieve statistical significance.

Variations in temperature and humidity also affected the number of females laying eggs, particularly at higher temperatures and lower humidity. On average, only 11% (113/102) of the females had their oviposition inhibited when kept at 25 °C. This number doubled at 30°C at both humidity settings (60% = 149/111; 80% = 100/75). At 35 °C, 1.6-fold more females had their oviposition inhibited at 60% humidity (100/55) in comparison to 80% (110/79). At temperatures of 25 and 30 ºC, approximately 44% of the females laid over 100 eggs. At the highest temperature (35 ºC), this number was reduced to 14.5% and 7.6% at 60% and 80% relative humidity, respectively (Table I). Despite being negatively affected by temperature, no significant effect from humidity was recorded for the daily oviposition pattern (60% relative humidity, F = 785.93, df = 333, p< 0.01; 80% relative humidity, F = 777.89, df = 273, p< 0.01).

The lifespan and number of surviving females varied under the different experimental conditions. The maximal survival period for females kept at 35 °C after feeding was 5 days. This period was two days longer in the group kept at 30 °C. At the mildest temperature (25 °C), lifespan was prolonged for up to 11 days and was strongly dependent on humidity (Table II).

Regression analysis revealed that survival is significantly reduced with largely the increase in temperature (R^2= 18.60%, b= -0.0649, df= 87, p< 0.01). The effect of the relative humidity on the lifespan was less evident (F= 0.1515, df= 110, p= 0.7000), althgout a pattern favoring survival at 25 and 35 °C was observed when females were submitted to the higher humidity, whereas the opposite was found in groups kept at 30 °C (Table II).

Oviposition time exhibited three distinct temporal patterns: the longest oviposition period occurred in females kept at 25 °C, regardless of humidity. At this temperature, oviposition was prolonged for up to 5 days, with an average of 52.9±6.19 and 75.01±8.12 eggs/female/day at 60% and 80% relative humidity, respectively. Females kept at 30 ºC and 60% humidity laid eggs up to three days, with a concentration of oviposition on the first day; only two females laid eggs on the third day. During the first two days, females maintained at 30 °C laid a similar number of eggs under both humidity settings. However, on the third day, 2.3-fold more eggs were laid at 80% humidity (117.67±10.04) in comparison to the lower humidity. The shortest oviposition period (2 days) was recorded at 35 ºC, in which 99% of the females laid their eggs three days after the blood meal. At this temperature,

Table I. Mean number of eggs laid by *Aedes aegypti* females under different temperature and humidity.

Tempe-ratures	60% rh		80% rh	
	Eggs mean±SE (n)	Oviposition variation (y)	Eggs mean±SE (n)	Oviposition variation (y)
25ºC	85.99±3.16 [a, B] (102)	4 – 160 (37.25%)	99.08±3.56 [a] (92)	4 – 155 (55.43%)
30ºC	82.89±3.33 [b, B] (111)	2 – 143 (37.84%)	75.75±5.03 [b] (75)	1 – 144 (45.33%)
35ºC	54.53±4.81 [c] (55)	1 – 126 (14.55%)	59.62±3.41 [c] (79)	2 – 132 (7.59%)
TOTAL	78.25±2.2 (268)		79.29±2.53 (246)	

n= number of females laid eggs. y= percentage of females with total ovipositions ≥100 eggs.
Capital letters indicate comparison of values in the same column and small letters show comparison among values in the same line. Regardless of the size same letters represent values without significant differences. Different letters means numbers statistic different (p < 0,05).

Table II. Variation in the oviposition patterns and survival rate (%) of *Aedes aegypti* females maintained in different temperatures and humidity.

Days	25°C 60% (ni= 113) EM±SE (S)	25°C 80% (ni= 105) EM±SE (S)	30°C 60% (ni= 149) EM±SE (S)	30°C 80% (ni= 100) EM±SE (S)	35°C 60% (ni= 100) EM±SE (S)	35°C 80% (ni= 110) EM±SE (S)
1-3	0 (100)	0 (100)	0 (100)	0 (100)	0 (100)	0 (100)
4	47.9±7.86 (100)	81.9±5.47 (100)	80.02±3.5 (100)	72.61±5.54 (100)	53.76±6.01 (100)	58.61±3.45 (100)
5	54.24±5.64 (96.46)	86.9±6.57 (97.14)	40.75±6.9 (57.4)	59.56±13.3 (39)	42 (12)	80 (20.9)
6	65.64±5.14 (89.38)	63.38±11 (85.71)	51.5±43.5 (33.3)	117.67±10 (8)	- (0)	- (0)
7	64.76±10.5 (64.6)	49.43±21.9 (67.62)	0 (5.55)	0 (1)	- (0)	- (0)
8	32±23 (23.01)	93.5±21.5 (34.29)	- (0)	- (0)	- (0)	- (0)
9	- (0)	0 (21.9)	- (0)	- (0)	- (0)	- (0)
10	- (0)	0 (8.57)	- (0)	- (0)	- (0)	- (0)
11	- (0)	0 (4.76)	- (0)	- (0)	- (0)	- (0)

ni= initial number of females. EM= egg mean. S= survival rate (%).

only one female in each setting laid eggs for two consecutive days, although about 21% and 12% of females kept at 80% and 60% humidity, respectively, were still alive in this period (Table II).

Fertility. The daily hatching rate under different temperature and humidity conditions is illustrated in Figure 1. The percentage of larvae obtained from eggs kept at 60% humidity reduced gradually with the increase in temperature (Figure 1A). At this humidity, eggs laid at 25 °C (2542 larvae/4050 eggs) led to about 10% and 20% more larvae than eggs laid at 30 °C (4324 larvae/7375 eggs) and 35 °C (513 larvae/1201 eggs), respectively ($F= 3.2925$, $df=2$, $p< 0.05$).

At the higher humidity (80%), egg viability remained similar at 25 and 30 ºC, with mean value of 58.88 ± 4.87% and 70.67 ± 5.56% (Figure 1B); there was a significant reduction at 35 ºC (43.08 ± 5.89) ($F = 51.002$, $df = 2$, $p < 0.05$). At both humidity settings, eggs kept at 25 °C for one week produced approximately twice as many males than females (60%: 1079/599; 80%: 453/257). The effects of temperature and humidity on other groups were less conclusive. At 60% relative humidity, eggs kept at 30 and 35 ºC led to a female to male ratio of 1:1.7 and 1:1.1, respectively. Inverse proportions were recorded for eggs kept at 80% humidity at these temperatures (female to male ratio at 30 ºC - 1:1.1; at 35 ºC - 1:2).

DISCUSSION

In the present study, the local *A. aegypti* strain proved sensitive to a low range of warmth (average 3 ºC), reducing egg production and survival as well as changing daily oviposition patterns with an increase in temperature. However, the intensity of the temperature effect was strongly associated to humidity. These results and the data in the literature demonstrate the role of temperature and humidity on mosquito population dynamics (Glasser & Gomes 2002; Miciele & Campos 2003; Beserra *et al.* 2006). High rates of adult mortality and decreased oviposition causing severe reductions mosquito densities have frequently been associated to a rise in temperature (Reeves *et al.* 1994; Oda *et al.* 1999; Alto & Juliano 2001; Afrane *et al.* 2006) and humidity (Canyon *et al.* 1999). In *Anopheles krombeini* (Huang, 1975), the fecundity and longevity of females were drastically reduced between 30 and 33.5 ºC when compared to individuals kept at 26 ºC (Joshi 1996).

The results of the present study also corroborate data in the literature indicating that other important mosquito features, such as daily oviposition pattern, hatching rate and sex proportion, are also influenced by these factors. The production of eggs was also dependent on humidity, with higher oviposition rates observed at the lowest temperature (25 °C) and higher humidity (80%). The inverse was obtained at 35 °C and 60% humidity, in which the number of eggs laid was severely reduced. Adult survival and hatching rate were also affected by the rise in temperature and lower humidity. These results suggest that the reduction in *A. aegypti* population density during hot, dry periods of the year is not only dependent on a reduction in breeding sites, but also is influenced by the effect of high temperature and low humidity on several aspects of mosquito biology. In fieldwork carried out in Recife, Regis *et al.* (2008) found *Aedes spp*. oviposition activity the year round, with marked fluctuations in time (means ranging from 100 to 2500 eggs per trap-cycle). However, egg density was generally higher from January to August, a period that includes the rainy season (May to August).

The higher oviposition rate recorded at the higher humidity agrees with results described by Canyon *et al.* (1999), who observed significantly higher oviposition rates in *A. aegypti* females kept at 84% relative humidity when compared to individuals submitted to lower humidity (34%). The reproductive cost caused under conditions of environmental stress may be due to the redistribution of nutrients to provide the individuals subsistence that would otherwise be used for egg production (Chadee 1997). This physiological modification can be compared to the gonotrophic dissociation induced by unfavorable environmental conditions (Omer & Cloudsley-Thompson 1970). Thus, blood normally used for egg production would be used for the survival of the females (Nayar & Sauerman 1975), thereby reducing fecundity during the unfavorable periods.

At mild temperatures (25 ºC), the period of oviposition can be extended for up to 5 days, resulting in an approximately 43% increase in the number of eggs in the environment when compared to conditions of high temperatures (35 ºC). These results suggest that *A. aegypti* populations in hot climates can nearly double in periods with mild temperatures. As this species can distribute the eggs of a same batch among several oviposition substrates (Reiter *et al.* 1995), it is likely that mild weather conditions would be the most favorable period for the dispersion of the mosquito. Variations in humidity appear not to influence the beginning or duration of the oviposition period, which exhibited a similar pattern in all experiments.

Higher temperatures reduced the survival of the females, although the differences were also dependent on humidity. When kept at 25 °C and 80% relative humidity, the lifespan was extended for up to 11 days. This number was reduced by half when submitted to 35 °C, regardless of the relative humidity. Adult dehydration caused by high temperatures and low humidity is likely to be the most important factor affecting survival (Nayar 1972; Reeves *et al.* 1994; Joshi 1996; Mogi *et al.* 1996) and could influence the population size of these insects in the environment (Alto & Juliano 2001). Under similar temperature conditions as those used in the present study (26 and 30 ºC and 80% relative humidity), *An. krombeini* females were found to survive an average of six-fold and four-fold more, respectively, than the *A. aegypti* females analyzed in the present study. However, at more adverse temperature conditions (35 ºC), *A. aegypti* demonstrates greater durability, surviving for five days longer when compared to *An. krombeini* females (Joshi 1996). Temperature and humidity variations contribute toward the dehydration of individuals, for which resistance to these phenomena is differentiated between species as well as strains of the same species (Mogi *et al.* 1996). According to Mogi *et al.* (1996), *A. aegypti* and *Aedes albopictus* (Skuse, 1894) in urban areas are more resistant to desiccation than cospecific strains in rural areas, suggesting that this attribute is important to the survival of these mosquitoes in urban areas where there is limited vegetation and low humidity.

Eleven days survival under 25 °C and 80% relative humidity observed in our work corroborate data described for *A. aegypti* reared at 27ºC 75% relative humidity and feeding on rodent blood deprived from suggar feeding (Harrington *et al.* 2001). Althought, in laboratory studies it is an usual practice to provide sugar to experimental mosquitoes (Gerberg 1970), several works have accumulated evidences that wild females do not need to feed on sugar to survive and reproduce (Edman *et al.* 1992; Van Handel *et al.* 1994; Costero *et al.* 1998). *A. aegypti* appears to be able to obtain the nutrients necessary for survival and reproduction by feeding frequently on blood (Van Handel *et al.* 1994; Scott *et al.* 2000).

High temperatures associated to low humidity also resulted in a decrease in the hatching rate of *A. aegypti* larvae. With the increase in temperature, a gradually smaller number of larvae were produced from eggs kept at 60% relative humidity. The opposite occurred at 80% relative humidity, at which there was an increase in hatching rate with the rise in temperature from 25 to 30 °C. An increase in the hatching rate associated to a rise in temperature has been reported in previous studies (Alto & Juliano 2001). Studying the hatching rate of *Anopheles albimanus* (Wiedemann, 1820), Ramsey *et al.* (1988) found that eggs kept at 30 ºC produced a larger amount of larvae than those kept at 25 ºC. This species deposits its eggs on the water surface in flooded oviposition sites exposed to intense sunlight. *A. aegypti* preferentially lays its eggs in the substrate on the border of oviposition sites in shady places. Therefore, *A. albimanus* eggs are more adapted to temperature variations, whereas *A. aegypti* eggs experience a greater impact from humidity.

In summary, the results regarding the effect of the temperature and humidity on the reproductive aspects of *A. aegypti* contribute toward the understanding of the population dynamics of this mosquito, particularly in hot areas, where the temperature in the summer often rises above 30 ºC. The greater concentration of *A. aegypti* in warm, rainy seasons is strongly influenced by the effects of temperature and humidity on several aspects of the mosquito lifecycle. The rise in population density favors the occurrence of epidemics in warm, rainy seasons, decreasing in drier periods, when the number of females in the environment is reduced.

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