

Life table characteristics of *Aedes aegypti* (Diptera: Culicidae) from Saudi Arabia

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Abstract. *Aedes aegypti* (= *Stegomyia aegypti*) mosquito is a world vector of important arboviral diseases like dengue and Rift Valley fever. Despite its wide distribution in the western and southern regions of Saudi Arabia, where dengue outbreaks have occurred, its ecology is largely unknown. In this study we report on the main life table developmental attributes of a laboratory colony of *Ae. aegypti* reared from field-collected larvae from Madinah Province, west of Saudi Arabia. Females were maintained on daily blood meal and sugar. The female fecundity was ~62 eggs/female at an overall rate of 72% hatchability. The mean time needed for eggs to hatch into larvae was 4.5 d. The mean pupation time (P_{50}) was 11.53 days (d). The proportion of immature survivorships were 0.69 for 1st larva to pupa (P/T), 0.98 for pupa to adult (A/P) and an overall 0.67 for 1st larva to adult (A/T). Males emerged faster than females with mean emergence time (E_{50}) of 12.83 and 15.31 d, respectively. The average developmental velocity (V) showed that males ($V=0.081$) developed faster than females ($V=0.068$). The male/female sex ratio at adult emergence was 0.48, and insignificantly different from the 1:1 ratio. The adult mean life expectancy at emergence (e_o) was 17.14 d for females compared to 9.59 d for males. The net reproductive rate (R_o) was 101.04 and the intrinsic rate of increase (r_m) was 0.15 with a mean generation time (G) of 30.7 d. The instantaneous mean of birth (B) and death rate (D) were 0.30 and 0.15, respectively, with r_m/B of 0.529 and B/D of 2.281. Compared to other *Ae. aegypti* strains from different geographic and ecological settings, the Saudi strain had a relatively low colonization potential. This is the first report on life table characteristics for *Ae. aegypti* from the Arabian Peninsula, and provides base-line information for wider studies on its natural populations. This is particularly important for understanding its population dynamics in relation to dengue transmission and control under regional conditions.

INTRODUCTION

Dengue is considered as the most rapidly-spreading mosquito-borne arboviral disease in the world with outbreaks reported as early as 1779 (Gubler & Clark, 1995; WHO, 2009). In the last 50 years there has been an estimated 30-fold increase in dengue incidence with increased expansion into new geographic regions and settings (e.g. from

urban to rural areas) in Asia, Africa and North and Latin America (WHO, 2009). Dengue fever is caused by four different virus genotypes (DEN-1 to 4) with variable epidemic activities and endemicity; with dengue hemorrhagic fever (DHF) as the most severe form. Its wide-spread tropical and subtropical distribution is highly linked to its mosquito vectors, the most important of which is *Aedes aegypti* (L.) (= *Stegomyia*

aegypti) and to a lesser extent *Aedes albopictus*. This is that renders controlling dengue largely dependent on the control of the mosquito vector populations (Gubler & Clark, 1995; Gubler, 1998, 2002; Scott & Morrison, 2003; Gratz, 2004; Morrison *et al.*, 2008; WHO, 2009; Wilder-Smith *et al.*, 2010).

Since the dengue virus was isolated for the first time from patients from Jeddah, west of Saudi Arabia, the Kingdom suffered three epidemics: 1994 (DEN-2), 2006 (DEN-1) and 2008 (DEN-3) (Fakeeh & Zaki, 2001, 2003; WHO/EMRO, 2005; Ayyub *et al.*, 2006; Zaki *et al.*, 2008). Most of the cases were dengue, with fewer cases of DHF, DSS (dengue shock syndrome) and death (WHO, 2009). Dengue fever continues to be a significant health problem in the western region of Saudi Arabia and usually linked to the proliferation of the mosquito vector populations following the rain season. The risk of dengue transmission is further amplified due to the peculiar demogeographic characteristics of the western region of Saudi Arabia. This region includes Makkah and Madinah, which contain the largest Islamic Holy places, the focus of millions of workers and visitors from all over the world, the most of them come through Jeddah province (Aziz *et al.*, 2012). The most of these expatriates are from disease-endemic countries. These conditions provide ideal opportunity for the introduction and increased transmission of dengue and other vector-borne diseases.

The mosquito life history parameters include female gonotrophic cycle and fecundity, egg hatching, birth and death rates, stage-specific survivorships, longevity and adult emergence (Grieco *et al.*, 2003). The life cycle characteristics of *Ae. aegypti* mosquitoes vary considerably with ecological particularities of each location. These include biotic factors such as population structure and dynamics, the presence of controphic species in larval habitats, the type and frequency of adult blood-meal and predators. The prevailing ecological factors include temperature, rainfall, type and number of larval water habitats, insecticidal applications, distance

from human dwellings etc (Rodhain & Rosen, 1997; Julio, 2009). Recent studies using molecular DNA markers revealed the presence of genetic differences among subpopulations of *Ae. aegypti* (Gorrochotegui-Escalante *et al.*, 2000; Paduan *et al.*, 2006; Julio *et al.*, 2009; Soliani *et al.*, 2010; Brown *et al.*, 2011). Different *Ae. aegypti* subpopulations have variable vectorial capacities for dengue viruses (Beerntsen *et al.*, 2000). These factors are critical determinants of vectorial capacity of the mosquito for disease transmission, and are essential for devising effective control strategies (Seawright *et al.*, 1979; Kenawy *et al.*, 1995; Grieco *et al.*, 2003; Tejerina *et al.*, 2009). Therefore, stage and age-specific horizontal life tables have been used to summarize the life history characteristics of a given species under different natural and controlled conditions (Reisen *et al.*, 1979; Reisen & Mahmoud, 1980; Grieco *et al.*, 2003).

Numerous life table studies were carried out on important vectors such as *Ae. aegypti* in order to gain information on population biology and dynamics, potential for colonization in the laboratory, vectorial capacity and impact on the risk of disease outbreaks and finally to determine the effect of habitat modification like deforestation or the effectiveness of various control measures on a specific species (Southwood *et al.*, 1972; Lansdowne *et al.*, 1975; Rueda *et al.*, 1990; Focks *et al.*, 1993a,b; Costero *et al.*, 1998; Grieco *et al.*, 2003; Afrane *et al.*, 2007; Carron *et al.*, 2008; Tejerina *et al.*, 2009).

Despite the presence of *Ae. aegypti* in Saudi Arabia and dengue outbreaks as well as the continuous active transmission of dengue, data are seriously lacking on vector populations from the Arabian Peninsula, particularly Saudi Arabia. Accordingly, the main purpose of this study was to determine the life-table characteristics of *Ae. aegypti* from the western region of Saudi Arabia. Such information is essential for better understanding of the population dynamics of this important arboviral vector, the dynamics of dengue transmission and control under local and regional conditions.

MATERIALS AND METHODS

Rearing of *Ae. aegypti* laboratory colonies

The *Ae. aegypti* colonies used in this study were established from larvae collected from small water bodies in the Madinah Province. The Madinah (Al-Madinah Al-Munawarah) Province is located in the western region of the Kingdom of Saudi Arabia (24°28' N, 39°36' E) (Fig. 1). It is ~ 600 km² in area at 340-400 km north of Makkah (Makkah Al-Mukarramah) and 150-190 km east of the Red Sea coast, with about 600 m above the sea level. It contains urban areas, mountains, valleys, slopes of torrents and desert, agricultural land, and arterial network. Madinah has a typical hot desert climate: dry and characterized by high temperatures ranging from 28-42°C in the summer and 11-24°C in the winter. The months of June-August are the hottest in the year with temperatures extremes above 45°C. The lowest temperatures are during December

and January. Generally, there is very little rainfall, which falls between November and May. The estimated average annual rainfall on Madinah is ~3.94 mm (range is 0 mm in September and 12.2 mm in April). The climate in Madinah is generally dry throughout the year except, with an average relative humidity of 22% (summer: 14%, winter: 40%) (NOAA, 2012 and MRM, 2013).

Colonies were established and maintained in an insectary thermostatically controlled at 25±2°C and 70±10% relative humidity (RH) and 8:16 hours light:dark cycle. Plastic cups of 10 cm diameter filled with 100 ml dechlorinated tap water, lined with filter paper were used as oviposition containers. Eggs were allowed to hatch in their oviposition containers and after 12-24 hrs, 50 larvae were transferred into larval pans, white round enamel pans (30 cm diameter) containing about 2 L dechlorinated tap water and left in the insectary for 24 hrs before use to acclimatize to the room temperature. Hatched larvae were fed

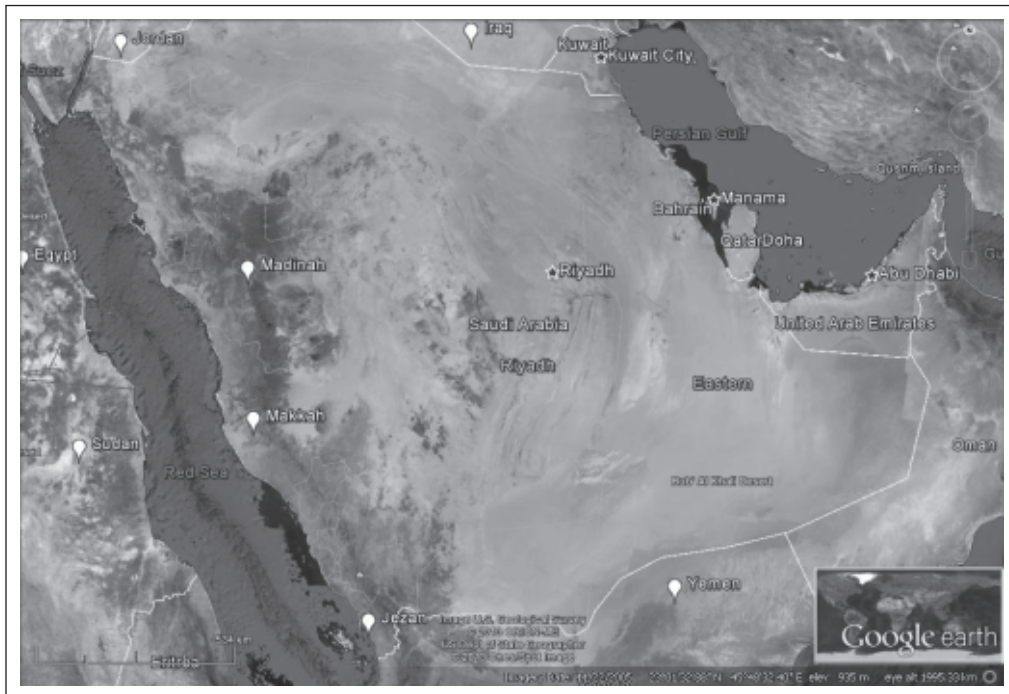


Figure 1. Map of Saudi Arabia showing Madinah region where *Aedes aegypti* larvae were collected to establish the laboratory colony used in this study. It also shows Makkah region. These regions include the Islamic Holy sites. Scale = 1:534 km. The map was designed by Google Earth 7 (7.0.1.8244, beta), 2012

Tetramine® powder (tropical fish food). The water was aerated daily using an air bubbler to avoid scum formation, and evaporated water was replaced as needed to maintain volume. Pupae were counted daily and transferred with an eye dropper to small plastic containers (10x10x7cm) covered with muslin netting and half-filled with water. These were placed in adult cages and observed for emergence of male and female adults. The adult cages were wooden-framed (60x60x60 cm) with a plywood base, covered with muslin netting with a cloth sleeve (40 cm long, 20 cm diameter) fitted to the front.

Calculation of *Ae. aegypti* life-table parameters

Life-table parameters were calculated according to the equations described (Southwood, 1972; Walter & Hacker, 1974; Reisen & Mahmoud, 1980; Kenawy *et al.*, 1995; Grieco *et al.*, 2003; Nur-Aida *et al.*, 2008).

Gonotrophic cycle

The duration of the gonotrophic cycles was determined as the time elapsed from blood feeding to oviposition. Human blood-fed females (2-3 d old) were placed individually in 400 ml screened plastic cups, lined with filter paper and containing 100 ml dechlorinated tap water, and were observed daily for oviposition. Females were offered a blood meal daily and 10% sucrose solution on a cotton pad. The number of eggs laid on the oviposition substrate was counted under a dissecting microscope and recorded daily to determine fecundity. The duration of the gonotrophic cycle was recorded.

Egg development and hatchability of *Ae. aegypti*

Egg development and hatchability were determined by transferring the egg batch of each female used for gonotrophic cycle determination to a 10-cm plastic cup half-filled with dechlorinated tap water and observed daily for hatching. The egg incubation period in days was estimated from oviposition till hatching. Another estimate for incubation period was expressed as the median hatching time (H_{50}) in days,

i.e., the time needed for 50% of eggs to hatch. This was calculated by fitting a regression of the form $P = a + b \cdot \ln(x)$; where P is the cumulative proportion hatched on each day (x) transformed to probits, a is the intercept and b is the slope or regression coefficient. The H_{50} was calculated from the equation $P = 50\%$ (Reisen & Mahmoud, 1980; Kenawy, 1991). Egg hatchability was expressed as the percentage of hatched eggs in a batch.

Development and survivorship of *Ae. aegypti* immature stages

Newly hatched first instar larvae derived from the same egg batch were counted, transferred to the larval pans and were fed Tetramine® as above. Larvae were transferred daily to a clean pan to avoid scum formation that might be lethal to larvae. Larvae were observed daily until all pupation and dead larvae were counted and removed from each pan. Pupae were collected daily, counted and transferred individually into specimen tubes containing dechlorinated tap water until adult emergence. The emerged adults were counted and sexed. The following developmental attributes were calculated as described (Reisen *et al.*, 1979; Kenawy, 1991). The median time in days for 50% pupation (median pupation time, P_{50}) and for 50% emergence of adult males and females (median adult time, E_{50}) were calculated as for H_{50} . The developmental velocity (V) for males and females were estimated at $1/E_{50}$. Survivorship was estimated from first instar larva to pupa (P/I), pupa to adult (A/P) and total survivorship from first instar larva to adult (A/I); where I is the number of first instar larvae at the start of the experiment; P is the number of pupae and A is the number of emerged adults. The sex ratio of emerged adults was estimated as the number of males relative to total emerged adults.

Estimation of adult longevity, survivorships, reproductive rate and generation time

For adult longevity (life expectancy, e_x) and age-specific survivorship rates (S), 10 replicates of 50 (3-4 d old) blood-fed females and 50 males were maintained in adult cages. Adult longevity at emergence (e_x) was

obtained from the following series of calculations:

$L_x = (I_x + I_{(x+1)})/2$; where I_x is the proportion of adults alive at beginning of day x , and $I_{(x+1)}$ is the proportion of mosquito adults alive at the beginning of the next day ($x+1$).

$I_x = y_x/y_0$; where y_x is the number of mosquitoes that were alive on day x and y_0 is the starting number of mosquitoes in the population.

$T_x = \sum_{i=1}^w L_x$: the total number of survivors beyond age x ; where w is the day when the last individual died.

$e_x = T_x/I_x$; where e_x is the adult life expectancy, i.e., the mean number of days remaining to the survivors at age x .

For net reproductive rate (R_0), intrinsic rate of increase (r_m), mean generation time (G), birth rate (B) and death rate (D), replicate sets of 10 blood-fed females were maintained individually in 400-ml screened plastic cups lined with filter paper and containing 100 ml dechlorinated tap water. Females were offered a blood meal daily, and all dead females were removed and recorded. The cups were examined daily for oviposition, and eggs counted. This procedure was continued until all females died, whereupon a life table was constructed. The net reproductive rate R_0 (the mean number of female offspring produced by a single female from a cohort during the course of its lifespan) was calculated from the formula: $R_0 = a \sum_{x=1}^w L_x m_x$; where I_x and w are as defined above, a is the proportion of females that survive from egg through adult emergence and m_x is the mean number of female progeny produced by a female of age x . The value of m_x was calculated using the formula: $m_x = E_x s$; where E_x is the mean number of eggs produced per female of age (x) and s is the proportion of these eggs that hatched into females.

The equation used to determine the intrinsic rate of increase per female, r_m , was modified from the Euler-Lotka equation (Mahmoud, 1997): $1.0 = \sum_{x=1}^w L_x m_x e^{-r_m(x+d)}$; where L_x , m_x and w are as defined above; e is the base of natural logarithms, x is the age by day and

d is length of time required for larval development from egg to adult emergence.

The mean generation time (G) was calculated from the equation: $G = Ln R_0 / r_m$. Since G includes d in its calculation, G is a realistic estimate of the time from mean oviposition in the present generation to mean oviposition in the offspring generation.

The instantaneous birth rate (B) was calculated from $B = ln(1+b)$; where b is the proportion of the population falling into age class (day) x and calculated as $1/b = \sum_{x=1}^w L_x e^{-r_m(x+1)}$. The death rate (D) was then calculated as $D = B - r_m$.

RESULTS

The life-table attributes measured for the Saudi *Ae. aegypti* strain under controlled laboratory conditions are shown in Table 1 and are summarized as follows.

Adult females began taking a blood meal approximately two days post emergence. The percentage of hatched eggs from the total oviposited (hatchability %) for each female ranged from 28.17% to 100% at a 72% overall hatchability. The female fecundity was ~62 eggs/female, with the mean time (H_{50}) needed for egg hatching into the first instar larvae of 4.51 d. There were no significant differences between H_{50} of different egg batches. The mean incubation period of eggs to develop (5.3 d) was not significantly different between females.

The mean pupation time (larval+pupal period) (P_{50}) was 11.53 d. The females emerged slower (E_{50} : 15.31 d) than males (E_{50} : 12.83 d), with males emerged first. The analysis of variance showed no significant difference between E_{50} for males and females ($F = 3.810$, $df = 9$ and $P = 0.065 > 0.05$). Males developed faster than females, with a slightly significant difference ($F = 4.65$, $df = 9$, $P = 0.044 < 0.05$). The mean length of the gonotrophic cycle was ~7 d.

The mean survivorship in the larva-pupa phase (P/I) was ~70% that is lower than in the pupa-adult phase (A/P) that reached 100%. The overall survivorship (A/I) was about 70% from the first larva to the adult stage. As shown in Figure 2, the age-specific

Table 1. Life-table attributes of *Aedes aegypti* mosquito from the western region of Saudi Arabia

Attribute	Mean±SD	Range
Gonotrophic cycle (in days)	6.56±1.32	5–9
Female fecundity (egg productivity)	62.18±17.67	41–95
Egg development		
Incubation period in days	5.3±1.85	3.0–8.0
Median time to egg hatch (H_{50}) in days	4.51±1.69	2.20–7.10
Hatchability %	72.04±26.83	28.17–100.0
Immature development		
Median pupation time P50 in days	11.53±2.52	8.95–17.45
Median emergence time E50 for ♂ in days	12.83±2.57	10.10–17.91
Median emergence time E50 for ♀ in days	15.31±3.34	11.89–22.93
Development velocity, (V) for ♂	0.081±0.015	0.056–0.099
Development velocity, (V) for ♀	0.068±0.013	0.044–0.084
Immature survivorships		
1 st Larvae to Pupae, P/I	0.69±0.22	0.236–0.90
Pupae to Adults, A/P	0.98±0.03	0.91–1.0
1 st Larvae to Adults A/I	0.67±0.22	0.225–0.878
Sex ratio of emerged adults	0.48±0.06	0.38–0.58
Adult mean longevity (at emergence, e_o)		
Males (n=10x50 ♂ ♂)	9.59±1.13	7.46–10.82
Females (n=10x50 ♀ ♀)	17.14±3.74	12.36–23.78
Net reproductive rate (R_o)	101.04±38.04	37.53–152.51
Intrinsic rate of increase (r_m)	0.15±0.02	0.112–0.194
Mean generation time (G)	30.7±4.58	25.34–38.04
Birth rate (B)	0.30±0.067	0.178–0.40
Death rate (D)	0.15±0.065	0.046–0.267
r_m/B	0.529±0.123	0.333–0.742
B/D	2.281±0.7	1.498–3.870

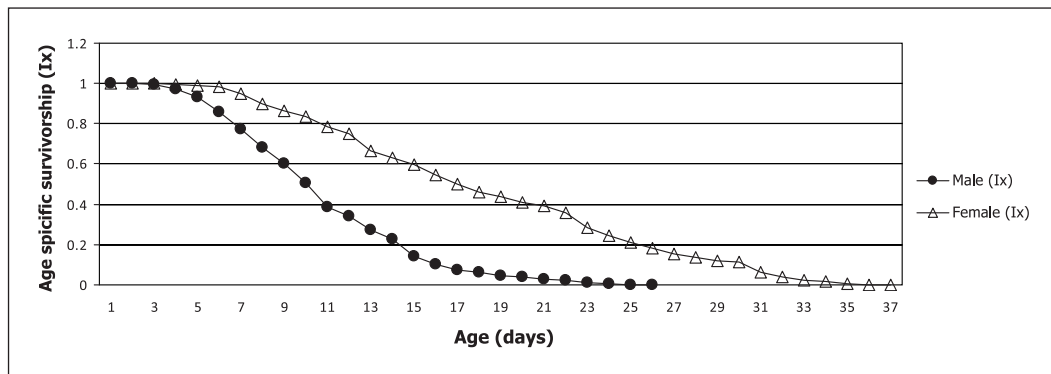


Figure 2. Age specific survivorship (I_x) for *Aedes aegypti* adult males fed 10% sucrose solution and females fed human blood and 10% sucrose solution

survivorship values (I_x) were similar for both males and females in the first 5 days post-emergence. The difference between males and females survivorship significantly increased with aging, where it reached 50%

for males at 10 d and for females at 20 d. It reached 0% survivorship (all individuals died) after ~27 and 37 d for males and females, respectively.

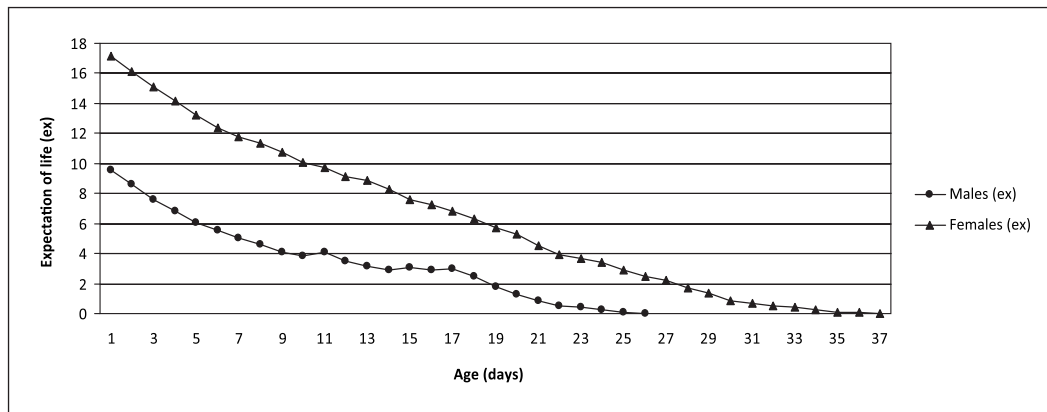


Figure 3. Expectation of life for established colonies of *Aedes aegypti* males and females as a function of age

The estimated adult life expectancy at emergence (e_o), showed that males had a significantly shorter life span than females ($F = 37.62$, $df = 9$, $P = 0.0000085 < 0.05$). The life expectancy (e_x) for females was higher than males, and gradually decreased for both sexes with increasing age till death (Fig. 3). The average sex ratio of emerged adults (0.48) was insignificantly different from the 1:1 ratio ($X^2 = 4.27$, $P = 0.51 > 0.05$).

The net reproductive rate (R_o) was 101.04 ± 38.04 d, with significant differences between the R_o means of each female offspring ($p < 0.05$). The mean intrinsic growth rate (r_m) was 0.15 with significant difference between each female offspring ($p < 0.05$). The mean generation time (G) was 30.7 ± 4.58 d with significant difference between the calculated mean generation times ($p < 0.05$). The mean birth rate (B) (0.30 ± 0.067 d) was higher than the death rate (D) (0.15 ± 0.065 d). The calculated r_m/B and B/D ratios were 0.529 ± 0.123 and 2.281 ± 0.7 , respectively. These results indicate the growth potential of this lab colony is relatively low.

DISCUSSION

The life table approach has been applied to study the survivorship and reproductive strategies of culicine mosquitoes including *Ae. aegypti* (Christophers, 1960; Crovello & Hacker, 1972; Southwood *et al.*, 1972; Lansdowne & Hacker, 1975).

The gonotrophic cycle of a female mosquito is defined as the time elapsed from blood feeding to oviposition. The duration of the gonotrophic cycle of mosquitoes is influenced by temperature and blood-meal type and frequency under natural or uncontrolled colonization conditions. Pant & Yasuno (1973), reported a duration of gonotrophic cycle of field collected *Ae. aegypti* as short as 3 d during the hot season in Bangkok, Thailand. This is much shorter than we reported for the Saudi *Ae. aegypti* colony (6.56 d) reared under controlled conditions. Christophers (1960) found that the gonotrophic cycle was regulated by temperature and the first oviposition was longer than the subsequent ones. It was noted that *Ae. aegypti* females used to take multiple blood meals during a single gonotrophic cycle (Yasuno & Tonn, 1970; Scott *et al.*, 1993, 2000). High temperature speeds up blood digestion and therefore, shortens the gonotrophic cycle duration, which might affect the vectorial capacity and disease transmission, as reported for the malaria vector in Kenya, *An. arabiensis* (Afrane *et al.*, 2007). Climate change and habitat modifications could lead to the movement of both human and vector populations. Due to these changes a vector species might be eliminated, while another one might be established in the new settings, with important implications for disease transmission (Afrane *et al.*, 2007).

The mean longevity values for the Saudi *Ae. aegypti* showed that males significantly lived (~10 d) shorter than females (~17 d), with a maximum generation time of 38 d. These estimates are in the range reported for strains from other geographical regions such as those from Argentina (males: 7.3-8.8 d; females: 11.5-58 d) (Tejerina *et al.*, 2009). The longest longevity (24 d) reported for the Saudi strain females is significantly shorter than those (58-116 d) for colonies reared under similar conditions (Christophers, 1960, Harrington *et al.*, 2001, Styer *et al.*, 2007, Tejerina *et al.*, 2009). Adult diet has variable effects on the longevity and fecundity of colonized vectors. Females fed blood lived up to 93 days, while those fed only sugar solution lived for a maximum of 12 d (Christophers, 1960). Female *Ae. aegypti* fed sucrose supplemented with nodihydroguariaretic acid lived longer than those reared on sucrose alone (Richie *et al.*, 1986). In addition, the mortality was significantly lower in females fed daily on blood than those fed every other day (Styer *et al.*, 2007). These differences in longevities or life expectancy were due to the different regime of feeding on blood and sugar, which in turn affected age-specific survival. In nature, other factors like predation and insecticidal applications also impact longevity and population densities, however, these are absent under colonization conditions. From life expectancy/longevity estimates of *Ae. aegypti* females and the length and number of gonotrophic cycles, females will take at least one blood meal. Assuming that most females take the first infected blood meal within 2 d post-emergence, they must live sufficiently long to support the virus incubation period (i.e., extrinsic incubation period, EIP) and become infective for transmission to take place (Salazar *et al.*, 2007).

The EIP is an important epidemiological indicator in disease transmission and is defined as the time required from the ingestion of virus by the mosquito till transmission to the next vertebrate host. Dengue virus took >11 d at a constant 25.88°C to complete development (Chowell *et al.*,

2007). In nature, these variations have important implications for the potential of the mosquito for dengue transmission and associated with its verifying epidemiological patterns (Harrington *et al.*, 2001; Styer *et al.*, 2007). The survivorships in the pupa-adult (A/P) phase reached 100% compared to ~70% in the larva-pupa phase and the overall survivorship (A/I) from the first larva to the adult stage. This is lower than those reported (98–100%) for four *Ae. aegypti* colonies reared under semi-natural conditions from Argentina (Tejerina *et al.*, 2009). The intrinsic rate of increase (r_m) and the net reproductive rate (R_o) are important indicators of the reproductive and growth potential of a given species (i.e. the number of progenies produced at specific time frame under certain conditions) as for multi-voltine species with overlapping generations (Hacker, 1972; Mahmood, 1997; Greico *et al.*, 2003; Nur-Aida *et al.*, 2008). Reisen *et al.* (1979) added that low r_m values are indicators of low evolutionary adaptation of the mosquito to existing or colonizing variable environments. These differ considerably between *Ae. aegypti* populations from different geographic regions, environmental conditions and experimental regimes. In our study, human blood meal with sugar solution was provided daily to females thus mimicking the natural environment. The R_o values (37.5-152.5 d) reported for the Saudi *Ae. aegypti* was higher than that (23 d) of a strain from Puerto Rico fed human blood and sugar during the hot season (Costero *et al.*, 1998). A range of R_o values (~84.6-113.4 d) was reported for *Ae. aegypti* from Brazil (Beserra & Castro, 2008). The r_m value calculated in this study for *Ae. aegypti* mosquito was 0.15 females per day, which is lower than the r_m values 0.24-0.92 for *Ae. aegypti* from Argentina (Beserra & Castro, 2008) and 0.21 d for *Ae. albopictus* from Malaysia (Nur-Aida *et al.*, 2008).

From their studies on anopheline mosquitoes, Greico *et al.* (2003) maintained the following observations: the r value increased with increased number of eggs (fecundity) laid in early days of adult life span and male ageing and succumbing. Birth and

death rates affect population growth rate and thus the colonization ability of a species. Age composition and adult survivorships (physiological age in relation to blood feeding) affect vectorial capacity. In *An. arabiensis*, high adult survivorships and reproductive fitness/fecundity increased the vectorial capacity for malaria transmission (Afrane *et al.*, 2007). Lower birth and death rates with lower r_m indicates the trend of a species towards population stability (Reisen *et al.*, 1979, Nur-Aida *et al.*, 2008). The Saudi *Ae. aegypti* strain has relatively low birth rate and a higher death rate, and the resultant $r_m B$ and B/D ratios were low. The low $r_m B$ and B/D ratios indicate the slow population growth and reduced colonizing ability, as previously reported for anopheline mosquitoes (Greico *et al.*, 2003). In contrast, *Ae. albopictus* had very low birth rate with a lower death rate, and the resultant $r_m B$ and B/D ratios were high, which indicated its very high colonizing ability and rapid population growth (Nur-Aida *et al.*, 2008).

Fecundity, in general, is the reproductive capacity of an organism or population, measured by the number of eggs or asexual propagates. Fecundity can increase or decrease in a population according to current conditions and certain regulating factors such as feeding times and the availability of a blood meal during the first gonotrophic cycle (Rai, 1964 and reviewed by Foster, 1995). Several other factors, for example, the size of females and hence the volume of blood meal also impacted the number of eggs produced by a female. In addition, adult diet type and frequency, female size, larval feeding and environmental conditions significantly affect both longevity and fecundity of colonized vectors (Rai, 1964; Briegel, 1990; Foster, 1995). Briegel, (1990), found that large *Ae. aegypti* females consumed blood as twice as that of small females, with a 4-fold increase in fecundity. He added that, the female body size was proportional to the efficiency of blood meal utilization for yolk synthesis and the amount of maternal reserves required for completion of oogenesis. *Aedes aegypti* females fed on blood and sugar during the hot season laid fewer eggs than females fed

on blood only (Costero *et al.*, 1998). Sugar feeding after a blood meal had no effect on *Ae. aegypti* fecundity during the first gonotrophic cycle, however, sugar was important for maternal energy reserves after oviposition (Zhou *et al.*, 2004). Fecundity is affected by the nutritional reserves accumulated during the immature stages; where reduced body reserves will result in poor quality adults. *Aedes aegypti* larvae fed a sub-optimal diet produced smaller adults with reduced ability to seek out a blood meal (Klowden *et al.*, 1988). Mosquito larvae maintained on high-protein diets produced large and highly-fecund females (Howell & Wilkins, 2007). Other factors that affect female fertility include the mosquito mating behavior in the confines of breeding cages as well as eggs laid by non-completely fertilized females (Foster & Walker, 2002; Impoinvil *et al.*, 2007).

The mean number of eggs produced by the Saudi *Ae. aegypti* females (~62 eggs/female) is in the range (47-307 eggs/female) recorded for other strains from different geographic regions like Argentina (Rai, 1964, Maciá, 2006, Tejerina *et al.*, 2009) and *Ae. albopictus* from Malaysia (mean 221 eggs/female) (Nur-Aida *et al.*, 2008). In our study, this significant decrease in the average female fecundity might be due to overcrowding, which has adverse effects on survival, rate of development and population growth (Andrewartha & Birch, 1954; Odum, 1959; Al-Misned, 2002). Temperature has been the most profound impacting factor on growth and survival of the developing embryo (Impoinvil *et al.*, 2007). The mean egg developmental time of *Ae. aegypti* under variable environmental conditions ranged between 2 to 7 d; where eggs develop faster in warm climates as in the tropics (Christophers, 1960; Southwood *et al.*, 1972; Foster & Walker, 2002). The mean time needed for the Saudi *Ae. aegypti* strain eggs to hatch into larvae (4.5 d) is in the range reported in other studies. Humidity also is a limiting factor in egg development and hatching; *Ae. aegypti* eggs exposed to 50% RH had significantly lower hatching rate than those kept under high humidity (Charles,

1960). *Aedes aegypti* eggs can survive long periods (months) of drought and as soon as submerged in water, they hatch (Nelson, 1986). This is one of the reasons that rendered the control of this species difficult. In general, the recorded values for the Saudi *Ae. aegypti* immature development from eggs to adult emergence were in the ranges (10-20 d) reported for other strains of *Ae. aegypti* or other species like *Ae. albopictus* under both field and laboratory condition (Christophers, 1960; Southwood *et al.*, 1972; Beserra & Castro, 2008; Nur-Aida *et al.*, 2008; Tejerina *et al.*, 2009).

The Saudi strain males emerged at 12.8 d faster than the females (15.3 d). The emergence time for both sexes is slower than that reported for Argentinean *Ae. aegypti* colonies (males: 7.2-8.1 d; females: 8.13-9.3 d) (Tejerina *et al.*, 2009). The sex ratio 0.48 of the Saudi strain of *Ae. aegypti* was close to the established ratio of 1:1 and similar to the ratio of an *Ae. aegypti* colony reared at $25.6 \pm 0.9^\circ\text{C}$ from Bernardo de Irigoyen, Argentina (Tejerina *et al.*, 2009). This result suggests that the Saudi strain has lower potential for colonization than the Argentinean strains, which were reared under simulated field conditions (i.e. uncontrolled temperature and RH% to mimic nature conditions).

In summary, life table models of a given mosquito disease vector species are important in providing primary information on its different developmental aspects under specific conditions either in the natural environment or in the laboratory. These models are essential for the understanding of life strategies of each species including life span, reproductive potential and stage-specific survivorships in response to biotic factors (food, host, presence of controphic species and predators) and abiotic factors (physicochemical characteristics of larval water habitats, climatic conditions, application of insecticides). The interactions between these factors determine the potential of this species to proliferate and its vectorial capacity for disease transmission. These life tables can be constructed under optimal or

controlled laboratory conditions. In this case, the information gathered will determine the colonizing potential of a species and maximum population growth in the absence of environmental pressures (species competitions, predators, insecticides) exerted on natural populations to keep their stability. This study provides the first report on the life parameters of *Ae. aegypti* strain from the Arabian Peninsula. This provides base-line information that is essential for wider studies towards better understanding of population dynamics of this mosquito under local and regional conditions. Such studies are critical for designing appropriate strategies for the reduction of this vector population to below the threshold needed for dengue virus transmission, with the main goal of minimizing the risk of outbreaks on local populations.

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