Serangga 22(1): 85-121
ISSN 1394-5130 © 2017, Centre for Insects Systematic,
Universiti Kebangsaan Malaysia

LIFE TABLE CHARACTERISTICS OF MALAYSIAN STRAIN *Aedes albopictus* (Skuse)

Rozilawati H[1,2], Mohd Masri S[3], Tanaselvi K[1], Mohd Zahari TH[1], Zairi J[2], Nazni WA[1], and Lee HL[1]

[1]Medical Entomology Unit, Institute for Medical Research, Jalan Pahang 50588 Kuala Lumpur, Malaysia
[2]Vector Control Research Unit, School of Biological Sciences, Universiti Sains Malaysia, 11 800 Pulau Pinang, Malaysia
[3]Strategic Resource Research Centre, Malaysian Agricultural Research Development Institute, PO Box 12301, 50744 Kuala Lumpur, Malaysia
Corresponding author: rozilawati@imr.gov.my

ABSTRACT

The survival of a mosquito is the most important aspect that affects its ability as a pathogen transmitting vector, such as *Aedes albopictus*, which is a vector of chikungunya and dengue. Knowledge on mosquito life demographics is important in providing a foundation for a successful vector control programme. In this study, two strains of *Ae. albopictus* [Selangor (SEL) and Kuala Lumpur (KL)] were employed in order to determine the life demographics, including the development period, survival rate, mortality rate, and reproductive capability undercontrolled laboratory conditions. A cohort life table was developed based on the data collected. The complete life cycle period was inconsistent and ranged between 6 to 14 days. The males have a shorter survival period compared

to the females. The percentage of females surviving and producing eggs has decreased across the gonotrophic cycle for both strains. A fluctuating pattern of oviposition among most of the females was observed throughout the gonotrophic cycle. The apparent mortality was highest at the embryogenesis stage than the other life stages across the gonotrophic cycle, with the pupae stage being recorded as the lowest mortality rate for both strains. Based on the demographic growth parameters calculated in this study, both strains showed favourable capability to be established in the laboratory. The data provided in this study can be used as a basic guideline on the population growth of the mosquito species and their capability as a pathogen vector.

Keywords: survival, *Aedes albopictus*, life table, gonotrophic cycle.

ABSTRAK

Kemandirian nyamuk merupakan aspek paling penting yang mempengaruhi kebolehannya sebagai vektor penyebar penyakit seperti *Aedes albopictus* yang merupakan vektor penyakit chikungunya dan denggi. Pengetahuan mengenai demografi hidup nyamuk adalah penting bagi menyediakan asas untuk program kawalan vektor yang berjaya. Dalam kajian ini, dua strain tempatan *Ae. albopictus* [Selangor (SEL) dan Kuala Lumpur (KL)] telah digunakan untuk menentukan demografi kehidupan, termasuk tempoh perkembangan, kadar kemandirian, kadar mortaliti dan keupayaan pembiakan di bawah keadaan makmal terkawal. Satu jadual hayat kohort telah dibangunkan berdasarkan data yang dikumpul. Tempoh kitaran hidup lengkap adalah tidak konsisten di antara 6 hingga 14 hari. Nyamuk jantan mempunyai tempoh hidup yang lebih pendek berbanding nyamuk betina. Peratusan nyamuk betina yang bermandiri dan menghasilkan telur didapati menurun menerusi kitaran gonotrofik.

Satu corak turun naik oviposisi telah diperhatikan bagi kebanyakan nyamuk betina sepanjang kitaran gonotrofik. Kadar mortaliti adalah paling tinggi pada peringkat embriogenesis daripada peringkat kehidupan lain di seluruh kitaran gonotrofik, dengan peringkat pupa mempunyai kadar kematian yang paling rendah bagi kedua-dua strain. Berdasarkan parameter pertumbuhan demografi yang dikira dalam kajian ini, kedua-dua strain menunjukkan keupayaan yang amat menggalakkan. Data yang disediakan dalam kajian ini boleh digunakan sebagai garis panduan asas kepada pertumbuhan spesies nyamuk ini dan keupayaan mereka sebagai vektor penyakit.

Kata kunci: kemandirian, *Aedes albopictus*, jadual hayat kohort, kitaran gonotrofik.

INTRODUCTION

The survivorship of a mosquito is the most important aspect that affects its capability as a pathogen vector. A study on life parameters such as developmental period/rate, survival and mortality rate, and reproduction of mosquitoes are important to understanding the population dynamic. The physical and biological mechanisms affecting the population can be understood and all data obtained can be used as a basic foundation for developing efficient and effective vector control strategies (Juliano, 2007)

A life table is a convenient and fundamental population model that can be constructed to understand the population dynamics of a species including the life demography and general biology, which include the survival, development, and reproductive system of a population under various conditions (Lansdowne & Hacker, 1975; Southwood, 1978; Reisen & Mahmood, 1980; Chi, 1988; Maharaj, 2003; Gabre, Adham, & Chi, 2005; Hu, Chi, Zhang, Zhou, & Zhang, 2010).

Through life table, predictions on population growth or decline can also be done (Erickson, Presley, Allen, Long, & Cox, 2010). Two types of life table are the age specific (horizontal) and time specific (vertical) (Southwood, 1978). The age specific or horizontal life table is more widely applicable for insects, (Southwood, 1978), because it provides a concise summary of survival, mortality and reproduction, and most insects have distinct generations and their populations are not fixed (Afrane, Zhou, Lawson, Githeko, & Yan, 2007; Southwood, 1978).

Studies have been done to study the mosquito life parameters with various factors influencing their survival, fecundity, and mortality including *Ae. aegypti* (Southwood, Murdie, Yasuno, Tonn, & Reader, 1972), *Cx. quinquefasciatus* (Walter & Hacker, 1974; Yao et al., 1988; Suman et al., 2011), and *Anopheles* sp. (Reisen & Mahmood, 1980; Maharaj, 2003; Okogun, 2005; Afrane et al., 2007; Olayemi & Ande, 2009).

The life parameters study of *Ae. albopictus* is still limited compared to *Ae. aegypti*, especially in Malaysia. In order to shed more light on the biology *of Ae. albopictus* such as development, survival, mortality and fecundity, experiments were conducted in order to determine the development period, the survival rate, mortality rate, reproductive capability and some of the demographic life parameters of selected strains of *Ae. albopictus* under laboratory conditions.

MATERIAL AND METHODS

Mosquito strains and experimental condition

Two *Aedes albopictus* Skuse strains were employed in this study which were the laboratory strain (SEL) and field strain of Kuala Lumpur (KL). For the laboratory strain, the mosquito originated from Selangor state has been continuously maintained for 40 generations (F40) in the insectarium during the study. For field strain, the first progeny produced from mosquitoes collected through ovitrap/larval surveillance from dengue prone areas in Keramat, Kuala Lumpur were employed (Rozilawati et al., 2015). They are colonized in the insectarium, of Medical Entomology Unit, Institute for Medical Research Kuala Lumpur under room temperature of 25 ±_1 ˚C and 75 ± 10% relative humidity and a photoperiod of 12:12 (light/dark) following the standard guidelines provided by the Institute for Medical Research, (2002).

Establishment of mosquito cohorts

This study was adapted from a study of transgenic *Ae. aegypti* fitness by Irvin et al. (2004) and Lee et al. (2009) with necessary modification. In this experiment, in order to get the virgin mosquitoes, the sex separations were done at the pupae stage.

A total of 50 males and 50 females of first pupae of each experimental strain were placed individually into glass tubes covering with fine netting containing 10 mL of dechlorinated water. Adult mosquitoes that emerged were designated as F0. Only 15 pairs of virgin mosquitoes which were the earliest 15 males and 15 females emerged were selected and paired in cages (23 cm X 23 cm X 23 cm) supplied with sucrose for mating purposes. The mosquitoes were allowed to mate for 72 hours before given a blood meal using a white mouse for 12 hours to ensure that the female had fully engorged. Two days (48 hours) after blood feeding, an ovitrap lined with filter paper with 225 mL of dechlorinated water was introduced into each cage.

The water from previous ovitrap was filtered using No 1 Whatman filter paper. The eggs were allowed to embroyonate by air drying at room temperatures for 7 days. The eggs were counted under a dissecting microscope and recorded accordingly. After counting, the filter papers were submerged into 15 individual trays containing 150 mL of dechlorinated water with larval food and covered with a mesh.

Immature development times and adult emergence

Only 10 larvae from each of the original 15 pairs were monitored for their developmental stage (larvae instar 1, 2, 3, 4, pupae). After the eggs were immersed in dechlorinated water for 24 hours, the 1st instar larvae were individually placed in glass tube with 10 mL seasoned water and larval food. The mean number of days at each stage was determined and compared between the strains using an independent *t* -test. The day the adults emerged was recorded separately by sex according to their parents. The emerged adults were labelled as F1.

The first 20 pairs (aged $\leq$ 2 days) of each strain were paired in standard cages (23 cm x 23 cm x 23 cm) only if they originated from the different F0 female to reduce the possibility of inbreeding effects. These 20 pairs (F1) were then used to assess the fitness of *Ae. albopictus* in relation to their survivorship, and more importantly, their fecundity status.

Adults' survivorship and fecundity

The survival and fecundity of the 20 pairs of F1 adult were monitored every 24 hours. Only 10% sucrose was supplied as a food source before and after blood feeding. The females were given blood meal 72 hours post mating. After feeding an ovitrap containing 225 mL seasoned water lined with filter paper was introduced in each cage for egg collection every 24 hour until 7th day post feeding. The water from ovitraps was then filtered using filter paper and then the filter papers were air dry at room

temperature for 7 days before the eggs were counted. The eggs were collected daily and counted. On the eighth days of post feeding, the blood meal was reoffered to the surviving females, and this process continued until all females die. The survivorship of the adult mosquitoes was recorded every 24 hours. The wings were measured from the apical notch to the axillary margin, excluding the wing fringe tip (Nasci, 1986; Mohammed & Chadee, 2011; Schneider, Chadee, Mori, Romero-Severson, & Severson, 2011) under a dissecting microscope (Leica EZ4 HD, Germany, magnification 20X) using the DIMAS 5.0 software.

The eggs were then submerged in 150 mL dechlorinated water in individual trays, and supplied with food as explained by Delatte et al. (2009). Any unhatched eggs were then considered as nonviable/sterile (Irvin et al., 2004; Lee et al., 2009). The number of survivors for each stage (larva to adult) for each female and each complete gonotrophic cycle (GC) were recorded. The sexes of adults emerged resulting from each GC for each female was also recorded. The survival percentage, the apparent mortality which is the measured mortality calculated as the numbers dying as a percentage of the numbers entering the stage (d_x as a % of l_x) and the real mortality which is calculated on the basis of the population density at the beginning of the generation (100 X d_i/l_c = the deaths in the *i*th age interval and l_c the size of the cohort at the commencement of the generation) were also calculated (Southwood, 1978; Suman et al., 2011).

Life demographic growth parameters

In order to calculate the life demographic growth parameters, the data of survivorship (larval to adult) and the daily fecundity of females were used to construct the *lxmx* life tables. The means and standard errors of the life table parameters were estimated using the jackknife method (Sokal & Rohlf, 1995). The following parameters were calculated (Birch, 1948; Southwood, 1978; Goodman, 1982; Price, 1984; Carey, 1993; Service, 1993;

Irvin et al., 2004; Yang& Chi, 2006; Nur Aida et al., 2008a; Nur Aida et al., 2008b; Suman et al., 2011; Sowilem et al., 2013):

i) $I_x = y_x/y_o$; the age specific survivorship, where y_x is the number of mosquitoes that were alive on day x and y_o is the starting number of mosquitoes in the population

ii) $L_x = (I_x + I_{(x+1)})/2$; where I_x is the proportion of mosquito 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).

iii) $T_x = \sum_{x=1}^{w} L_x$ total number of survivors beyond age x;

where w is the day when the last individual died

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

v) *GRR* = the gross reproductive rate

vi) $R_0 = \alpha\sum_{x=0}^{w} l_x m_x$ the net reproductive rate where l_x is the fraction of females alive at age x and m_x is the number of daughters born to survive females at age x. $R_o > 1.0$ the population increased in size, $R_o < 1.0$ population growth is declining.

m_x is the mean number of female progeny produced by a female of age x. The value of m_x was calculated as $m_x = E_x s$, where E_x is the mean number of eggs produced per female of age x, s is the proportion of these eggs that are female (assumed to be equal to 0.5).

vii) r_m = The intrinsic rate of natural increase (the maximum exponential rate of increase by a population growing within defined physical conditions). It is estimated by using the iterative bisection method from Euler-Lotka equation:

$$1 = \alpha\sum_{x=0}^{w} l_x m_x e^{-r(x+D)}$$

viii) λ = EXP r_m, finite rate of increase

ix) $T_c = \sum l_x m_x / R_o$; The mean generation time (average interval separating births of one generation from the next generation)

x) $T_d = \ln(2)/r_m$, the doubling time in days (the time required by a population growing exponentially without limit to double in size when increasing at a given r_m.

The mean jackknife estimates of demographic parameters were then compared using independent *t*-test (p = 0.05) using SPSS 17.00 to determine any significant difference in the population growth parameters between both mosquito strains.

RESULTS

Immature development period

All 15 females of SEL and KL strains laid 1153 (76.7 ± 13.66) and 772 (51.5 ± 12.2) eggs respectively**.** The SEL strain oviposited all their eggs within 3 to 5 days post feeding and KL strain oviposited all their eggs within 3 to 7 days post feeding**.** From the immature development period experiments, it was determined that there was a significant difference between both strains at several life stages with inconsistently shorter or longer period between both strains at the life stage. There was no significant difference in the development period between both strains during larva instar 1 and instar 2. The L1 stage only

needed 1 day for both strains, whereas the L2 spent only 1 to 2 days (SEL and KL strain). SEL strain took significantly a shorter period during the larva instar 3 than KL strain, $t(271) = -7.182$, $p < 0.00$. The L3 recorded a minimum of 1 day and maximum of 2 days for both strains. Whereas the KL strain took significantly shorter period during the larva instar 4, $t(269) = 5.108$, $p < 0.05$) and pupa, $t(262) = 8.954$, $p < 0.05$). The L4 stage recorded a minimum of 1 day to a maximum of 5 days for the SEL strain, and a maximum of 4 days for the KL strain. The SEL strain spent 2 to 4 days in the pupal stage, but 1 to 4 days for the KL strain. However, it was determined that the SEL strain took significantly shorter period to develop from the larva instar 1 to adult eclosion than the KL strain, $t(258) = -6152$, $p < 0.00$. Both strains tested were able to complete their life cycles from L1 to adult eclosion within 6 – 11 days for the SEL strain and 8-14 days for the KL strain. The emerging times of males and females were significantly different between both strains. The males of SEL strain took a significantly shorter period than the KL strain, $t(130) = -5.080$, $p < 0.00$. The same with the females, where the SEL strain emerged significantly faster than the KL strain, $t(126) = -4.651$, $p < 0.05$. For the SEL strain, the male emerged between day 6 to 9 and females emerged between day 7 to 11, whereas for the KL strain, the males emerged between day 8 to 13 and day 8 to 14 for the females. Males emerged approximately 1 day before females for both strains. The ratio of males and females emerged were close to one for both strains. The SEL strains produced 0.94:1.00, whereas the KL strain produced 1.13:1.00 (males to females). The mean development period (day) for each life stages for both strains were summarized as in Table 1.

Table 1. The mean development time (days) and emerging times of males and females of the *Aedes albopictus* Skuse SEL and KL strains

		SEL strain Mean ± SE	KL Strain Mean ± SE
Development time (days)	Instar 1	1.0 ± 0.0[a]	1.0 ± 0.0[a]
	Instar 2	1.0 ± 0.0[a]	2.0 ± 0.0[a]
	Instar 3	1.5 ± 0.1[a]	1.9 ± 0.1[b]
	Instar 4	2.0 ± 0.1 [a]	1.6 ± 0.1[b]
	Total larva	5.5 ± 0.1[a]	6.5 ± 0.1[b]
	Pupa	3.0 ± 0.1[a]	2.4 ± 0.1[b]
	L1 to adult eclosion	8.4 ± 0.1[a]	9.1 ± 0.1[b]
Emerging time (days)	Male	8.1 ± 0. 1[a]	8.8 ± 0.1[b]
	Female	8.7 ± 0. 1[a]	9.5 ± 0.2[b]

Means followed by different letters among rows are significantly different ($p < 0.05$), (Independent *t*-test test).

Survival of adult mosquitoes

The longevity of adult males were not significantly different between the SEL (24.9 ± 2.6) and KL strains (28.0 ± 2.2), $t(38) = 0.522$, $p > 0.05$. Similarly, there was also no significant difference in the adult females longevity between the SEL (31.3 ± 3.0) and KL strains (33.6 ± 3.2), $t(38) = 0.897$, $p > 0.05$. However, overall adult females lived longer than the males for both strains tested and the duration from 10 - 68 days and 13 - 52 days for the females of the SEL and KL strain respectively. The longevity of the SEL strain males ranged from 9 - 40 days while the KL strain ranged from 10 - 49 days. The life expectancy (at emergence) of SEL and KL strain females calculated was 26.1 and 33.1days respectively, whereas for the SEL and KL strain males it was 25.4 and 28.5 days, respectively. The age specific survivorship for the adult mosquitoes used in this study declined through time for both sexes and strains as shown in Figure 1.

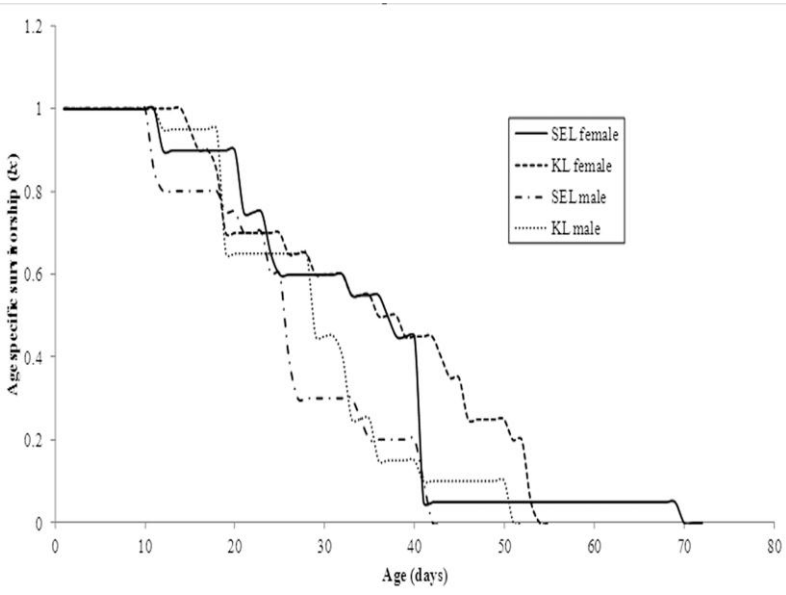

Figure 1. Age specific survivorship (*lx*) for adults of both strains and sexes of *Aedes albopictus* Skuse

Female survival, fecundity, and mortality rates

The SEL strain produced significantly more eggs (4 421, 245.6 ± 24.1) than the KL strain (2 726, 151.4± 29.4) during their lifetimes, $t(34) = 2.479$, $p < 0.05$. The females of the SEL strain oviposited a minimum of 56 eggs and a maximum of 402 eggs per female for the entire GC; whereas for the KL strain, a minimum of 3 eggs and a maximum of 414 eggs were oviposited per female for the entire GC. A fluctuating pattern of oviposition among most of the females was observed throughout the GC. A total of 11 (55%) and 9 (45%) females for the SEL and KL strains, respectively, showed a fluctuating pattern of oviposition. The pattern was more obvious for 1 SEL strain female and 3 KL strain females which lived and oviposited the longest among them. Others recorded increased, decreased or single number of eggs oviposited across the GC.

The number of females survived and producing eggs decreased across the GC for both strains. The females of the SEL strain survived and produced eggs up until the 7th GC, in which 1 of the female were able to complete the 7th GC before mortality. After the 8th feeding, the female died at 68 days post emergence. The females of the KL strain survived until the 6th GC, with 15 % (3) survival and producing eggs before mortality. Across the GC, overall, the eggs oviposited declined for both strains. However, an increase in fecundity was recorded at GC2 for the KL strain and GC7 for the SEL strain. The SEL strain produced more eggs than the KL strain until the 4th GC; however, during the 5th to 6th GC, lower numbers were oviposited by the strains since only one female SEL strain oviposited egg during that period compared to three females for the KL strain (Table: 2).

The stage specific survivorship rates (eggs to adult eclosion) fluctuated across the GC with the highest recorded at GC 5 for the SEL strain and GC 4 for the KL strain. Even though a slight increase in the number of eggs was recorded at the last GC (GC 7 for SEL strain and GC 6 for KL strain) the percentage of adults survived decreased from the previous GC. Overall, the same observation was made for the sex ratio of the F1 cohort, the females and males proportion were close to 1:1 across the GC except for GC 4 (KL strain), in which more males emerged than females. Both apparent and real mortality were highest at the embryogenesis stage than the other life stage across the GC. The same scenario was determined for the entire life period (total GC). The pupal stage recorded the lowest mortality rate for both strains (Table 3 and 4).

On average females were bigger than males. However, based on the independent *t* -test, there was no significant difference between the size of females of the SEL strain (2.50 ± 0.02) and the KL strain (2.52 ± 0.0.03) , $t(38) = 0.067$, $p > 0.05$ and also between the size of males of the SEL strain (2.04 ±

0.04) and the KL strain (2.03 ± 0.04), $t(38)=0.876$, $p > 0.05$ used in this study.

Table 1. Eggs oviposited by females *Ae. albopictus* for SEL and KL strain across the gonotrophic cycle

GC	Strain	N	Total	Mean ± SE
1	SEL	18	1312	72.9 ± 6.6
	KL	18	686	38.1 ± 6.9
2	SEL	16	1265	79.1 ± 9.3
	KL	14	809	57.8 ± 10.6
3	SEL	12	897	74.8 ± 7.3
	KL	9	463	51.4 ± 10.0
4	SEL	11	753	68.5 ± 6.2
	KL	8	342	42.8 ± 11.5
5	SEL	1	67	67.0 ± 0.0
	KL	6	279	46.50 ± 3.70
6	SEL	1	43	43.0 ± 0.0
	KL	3	147	49.0 ± 4.7
7	SEL	1	84	84.0 ± 0.0

*N= number of females oviposited eggs

Table 2. Stage specific survivorship and mortality rates for *Aedes albopictus* Skuse SEL strain

GC	Parameter	Egg	Larva	Pupa	Egg-Adult	Female
1	% Survival	43.29	75.00	96.48	31.33	52.07
	% Apparent mortality	56.71	25.00	3.52		
	% Real mortality	56.71	10.82	1.14		
2	% Survival	52.02	77.36	91.16	36.68	60.13
	% Apparent mortality	47.98	22.64	8.84		
	% Real mortality	47.98	11.78	3.56		
3	% Survival	59.87	63.50	87.98	33.45	53.00
	% Apparent mortality	40.13	36.50	12.02		
	% Real mortality	40.13	21.85	4.57		
4	% Survival	44.89	65.38	97.29	28.55	57.21
	% Apparent mortality	55.11	34.62	2.71		
	% Real mortality	55.11	15.54	.80		
5	% Survival	67.16	95.56	100.00	64.17	55.81
	% Apparent mortality	32.84	4.44	.00		
	% Real mortality	32.84	2.99	.00		
6	% Survival	65.12	89.29	100.00	58.14	48.00
	% Apparent mortality	34.88	10.71	.00		
	% Real mortality	34.88	6.98	.00		
7	% Survival	44.05	100.00	100.00	44.05	70.27
	% Apparent mortality	55.95	.00	.00		
	% Real mortality	55.95	.00	.00		
Total	% Survival	50.01	72.46	93.32	33.81	55.99
	% Apparent mortality	49.99	27.54	6.68		
	% Real mortality	49.99	13.78	2.42		

Table 3. Stage specific survivorship and mortality rates for *Aedes albopictus* Skuse KL strain

GC	Parameter	Egg	Larva	Pupa	Egg-Adult	Female
1	% Survival	74.69	70.50	99.11	52.19	53.29
	% Apparent mortality	25.31	29.50	0.89		
	% Real mortality	25.31	22.03	0.47		
2	% Survival	49.38	77.72	98.21	37.69	46.72
	% Apparent mortality	50.62	22.28	1.79		
	% Real mortality	50.62	11.00	0.69		
3	% Survival	47.33	71.30	99.39	33.54	62.58
	% Apparent mortality	52.67	28.70	0.61		
	% Real mortality	52.67	13.58	0.21		
4	% Survival	77.95	100.00	94.19	73.41	26.75
	% Apparent mortality	22.05	0.00	5.81		
	% Real mortality	22.05	0.00	4.53		
5	% Survival	47.24	80.83	96.91	37.01	54.26
	% Apparent mortality	52.76	19.17	3.09		
	% Real mortality	52.76	9.06	1.18		
6	% Survival	37.15	94.39	98.02	34.38	50.51
	% Apparent mortality	62.85	5.61	1.98		
	% Real mortality	62.85	2.08	0.69		
Total	% Survival	56.93	79.64	97.65	44.28	49.05
	% Apparent mortality	43.07	20.36	2.35		
	% Real mortality	43.07	11.59	1.06		

Demographic growth parameters

Significant differences were determined among the demographic parameters generated from jackknife $l_x m_x$ data for both strains. The gross reproductive rate (*GRR*), $t(38) = 4.255$, $p < 0.05$, the net reproductive rate (R_o), $t(38) = 2.605$, $p < 0.05$, the intrinsic rate of increase (r_m), $t(38) = 3.730$, $p < 0.05$ and the finite rate of increase, (λ) $t(38) = 3.780$, $p < 0.05$, for the SEL strain was significantly higher than the KL strain. The mean generation time (T_c), $t(38) = -2.089$, $p < 0.05$ and doubling times in days (T_d), $t(38) = -3.086$, $p < 0.05$ were significantly lower for the SEL strain than the KL strain (Table 5). Based on these values, both strains were found to increase in size where the R_o values were more than 1.0 and increased as shown in Figure 2.

Table 4. Demographic growth parameters for the SEL and KL strains *Aedes albopictus* Skuse

Parameter	SEL strain	KL strain
GRR	213.6 ± 10.9^a	104.2 ± 17.8^b
R_o	118.6 ± 14.9^a	65.4 ± 13.9^b
r_m	0.24 ± 0.01^a	0.18 ± 0.01^b
λ	1.27 ± 0.01^a	1.21 ± 0.01^b
T_c	19.8 ± 0.6^a	22.3 ± 1.1^b
T_d	2.8 ± 0.1^a	3.7 ± 0.2^b

Means followed by different letter within row are significantly different at $p < 0.05$ (independent *t*-test)

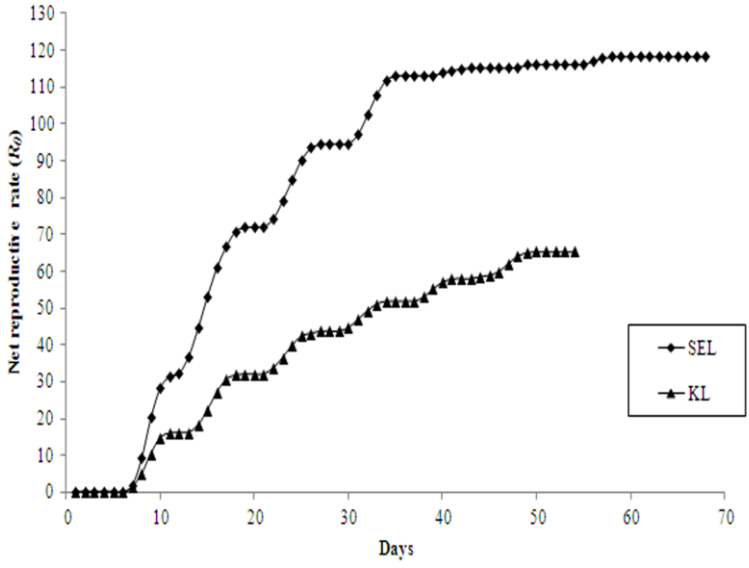

Figure 4 Cumulative net reproduction rate (R_o) of *Aedes albopictus* Skuse for Selangor (SEL) and Kuala Lumpur (KL) strains

DISCUSSION

In this present study, it was determined that the immature development periods for both strains were inconsistently shorter or longer in both the SEL and KL strains. Both tested strains were able to complete their life cycles from L1 to adult eclosion within 6 – 11 days for the SEL strain and 8-14 days for the KL strain. The result obtained was within the findings of previous studies such as Abu Hassan & Yap (1999), who recorded the developmental period of *Ae. albopictus* from egg to adult between 6 to 8 days, and Lee (2000) who determined that at

ambient temperature, *Ae albopictus* could complete its life cycle from egg to adult between 9 to 10 days. It was also reported by Manorenjitha (2006) that *Ae. albopictus* collected from Penang Island exhibited a developmental period (from larval to adult stage) of about 7 to 8 days with the pupal stage lasting 1 to 2 days under laboratory condition. Mosquito developmental period is reportedly affected mainly by temperature, oxygen tension, food supply, density or crowding, and sex (Ho et al., 1972; Hien, 1975; Hawley, 1988; Estrada-Franco & Craig, 1995). Even though this present study was conducted under laboratory conditions with stable temperature and relative humidity, sufficient food supply, and ample space to avoid overcrowding, the developmental period was within the range of that conducted in the field in this region, e.g. ovitrap surveillance conducted in Singapore, whereby the mean time from oviposition to adult emergence was about 19 days (Chan, 1971; Hawley; 1988). The study conducted by Nur Aida et al. (2008a) on the life table of the immature stages of *Ae. albopictus* in a wooded area in Penang Island, recorded a developmental time of between 6 to 10 days from eggs to adult eclosion.

In the present study, the emergence times of males and females were significantly different between both the SEL and KL strains. For the SEL strain, the male emerged between day 6 and 9 days and the females emerged between day 7 and 11days; whereas for the KL strain, the males emerged between day 8 and 13 days and the females between 8 and 14 days. The males emerged approximately 1 day before the females for both strains. Males usually emerged earlier than females since the males have to prepare themselves prior to mating. Contrary to the females, the males are not sexually matured at emergence as they have to rotate their hypopygium through 180° before ready

to mate, which usually takes about 1 day (Becker et al., 2010). The emergence period for both sexes of adults obtained in this present study was found to be within the range of the study conducted by Tsuda et al. (1994). They reported an emergence periods of 6.4 to7.5 days for males and 7.5 to 8.5 days for females of the Chiangmai and Nagasaki strains *Ae. albopictus* with most of the males emerged before the females (at 27 °C, 75% R.H, laboratory conditions). Study by Mori (1979) showed that females took 9.8 days and males 8.7 days to develop at 25˚C.

Life expectancy is an important aspect of mosquito populations in relation to their survival and probability as vectors of pathogens (Suman et al., 2011). The present study indicated that the females of both strains lived longer than the males and the maximum longevity from emergence recorded for females was 68 days (SEL strain) and 52 days (KL strain) and the life expectancy calculated was 26.10 days (SEL strain) and 33.1 days (KL strain). A previous laboratory study on the survival of *Ae. albopictus* reported that the females lived longer than the males, from 4 to 8 weeks up to 3 to 6 months whereas males lived from 6 days to a maximum of 68 days (Hawley, 1988). Result of the present study closely resembled that of Gubler & Bhattacharya (1971), who reported an average life expectancy of 38 days (maximum 73 days) for females and 30.3 days (maximum 68 days) for males under 26˚C and 50 - 60% relative humidity. The study by Tsuda et al., (1994) indicated a longevity of 16.9/ 28.7 days for the males and 30/31.7 days for the females of the Chiangmai and Nagasaki strains of *Ae. albopictus*, which was slightly shorter than reported in the present study. The same were reported by Lee (2000) and Nur Aida et al. (2008b). The former reported a male longevity of 10 to 22 days (mean 16 days) and a female longevity of 12 to 40 days (mean 26 days). Whereas the latter, reported a life

expectancy of 19.47 days for females and 10.17 days for males under uncontrolled laboratory conditions. Besides temperature, the survivorship of mosquitoes is also influenced by the nutrition provided (Hawley, 1988; Clements, 1992). Previous study indicated that the longevity of female mosquitoes provided with 10% sucrose solution after blood meal was longer or higher than those only provided with water after blood feeding (Xue et al., 2008). The sucrose solution provided was also important for male fitness, since the males needed the sucrose to have sufficient reserve in nature mainly for survival, dispersal, and mating (Puggioli et al., 2013).

In this study, both sexes of mosquito were continuously provided with 10% sucrose solution (females after blood meal) to ensure they can survive with sufficient food supply. Briegel & Timmermann (2001) also indicated that *Ae. albopictus* utilized only 35 - 50% of blood protein for oogenesis and the rest might be used for their maintenance, thus influencing their longevity. The survivorship of adult mosquitoes especially females are very important since the survivorship is closely related to their capability as vectors of pathogens. Dubrulle et al. (2009) reported that *Ae. albopictus* and *Ae. aegypti* could be infected with the chikungunya virus as early as two days after ingestion of infectious blood meal, and are able to transmit the dengue virus at day 9 post infection (Vega-Rua et al., 2013). With a life expectancy of 26.10 (SEL strain) and 33.10 (KL strain) days, the probability of the mosquitoes transmitting the virus is sufficiently high. In a separate study by Reiskind et al. (2010) comparing the longevity of infected and uninfected *Ae. albopictus* with chikungunya virus, they reported a significant reduction in the life span of the infected mosquitoes. The average life span was 54.77 days for uninfected and 45.19 days for infected mosquitoes, which are longer than reported in the present study. The longevity or survivorship of adult mosquitoes can be shorter in nature. However, *Ae. albopictus* tends to take

multiple blood feedings (Hawley, 1988; Estrada-Franco & Craig, 1995; Ponlawat & Harrington, 2005; Delatte et al., 2010; Farjana & Tuno 2013) to complete their GC, an aspect that should be taken into consideration, when correlating the longevity and the capability to transmit pathogens in nature.

In the present study, reproduction by the females was evaluated; the females of the SEL strain oviposited a mean of 245 eggs with a minimum of 56 and a maximum of 402 eggs per female for their entire life span, whereas for the KL strain, a mean of 151 was oviposited with a minimum of 3 and a maximum of 414 eggs oviposited per female. Previous studies have reported various lifetime fecundity for *Ae. albopictus*, as many as 950 (Galliard, 1962; Hawley, 1988), 784 (Gubler & Bhattacharya, 1971), 124 (del Rosario, 1963) eggs, with some reported average of 300 to 345 eggs (Gubler, 1970; Gubler & Bhattacharya, 1971; Hien, 1976), 283 (Gubler & Bhattacharya, 1971), 221 (Nur Aida et al., 2008b), 105 and 84 (Hamady et al., 2013), 77 (Nur Aida et al., 2011) and 46 eggs (del Rosario, 1963). The fecundity of female mosquitoes may depend on various factors such as host species(Moore & Fisher, 1969; Gubler, 1970; Chan, 1971; Hawley, 1988; Xue et al., 2008), larval/adult nutrition (Yamany & Adham, 2014) the pupal mass or adult size (Armbruster & Hutchinson, 2002), rearing condition such as density (Reiskind & Lounibos, 2009) and also geographical differences (Leinsham, Sala, & Juliano, 2008; Suman et al., 2011). Body size has been positively correlated with female fitness especially fecundity (Blackmore & Lord, 2000; Briegel & Timmermann, 2001). Even though the size of females used in this study was not significantly different, the total fecundity of the SEL strain females was significantly more/higher than the KL strain females. This may be because the SEL strain was already a laboratory adapted strain and the KL strain was a field strain that was still adapting to the laboratory conditions and might utilize their blood protein as

energy source for maintenance and their survival in a new environment (Leinsham et al., 2008; Dieng et al., 2010)

Overall, the fecundity decreased with increasing GC, a situation which was also reported in previous studies (Galliard, 1962; Chan 1971; Gubler & Bhattacharya, 1971; Hien, 1976; Dieng et al., 2010). However, an increase was recorded for GC2 (KL strain) and GC7 (SEL strain). Even though the number of surviving females also decreased across the GC, which affected the total number of eggs deposited by the females, it was also determined that some of the females had fluctuating oviposition patterns throughout the GC, especially for females that lived more than 4 GC. This situation was also reported by Gubler & Bhattacharya (1971), who documented that the total and average fecundity per GC in *Ae. albopictus* Calcutta strain fluctuated and females with fluctuating oviposition patterns survived the longest. Since the adult size was not significantly different between the two strains, it seemed that the larval rearing condition was not the limiting factor because both were reared under similar nutritional and spatial conditions. Even though females could retain eggs for the next oviposition, the possibility however was very minimal (Packer & Corbet, 1989). In this experiment blood meal was provided at an interval of 7 days from the previous blood feeding and all mosquitoes were observed to oviposit all their eggs within 3 to 6 days of post feeding; therefore, it was considered that the eggs oviposited at each GC were produced from each blood meal. In the field, it was reported that based on the parous rate data, females *Ae. albopictus* only matured on average a single batch of eggs (Hawley, 1988), and fecundity in the first GC was assumed to have a direct relationship with lifetime fecundity (Leinsham et al., 2008). However, based on the fluctuating pattern of fecundity in this study, the first GC might not be a good indicator of the species lifetime fecundity. This result was also supported by the study by Leinsham et al.

(2008) who found a very weak correlation between early fecundity (first GC) and the residual reproduction for three strains of *Ae. albopictus*.

The highest mortality of *Ae. albopictus* was recorded at the egg stage during which the larvae failed to hatch, compared with the other stages throughout the study, and the lowest recorded was at the pupal stage. The same observation was reported by Irvin et al., (2004) and Lee et al., (2009); in assessing the fitness of transgenic *Ae. aegypti*, they found that the mortality was greatest for the transition from egg to the larval stage. In a study conducted in an uncontrolled condition insectarium, Nur Aida et al., (2011) found that the highest mortality of *Ae. albopictus* was also during the egg stage, followed by the larval and pupal stages. The mortality of these immature stages might be due to various factors such as infertility, environmental conditions such as temperature and the oxygen tension, predation, and culture condition (Okogun, 2005). In this study, the eggs that failed to hatch were considered sterile/infertile, the factor that caused the mortality. Predation and/or parasitism factors were excluded in this study; however, it should be considered in the field condition. It is not surprising that the pupal mortality was the lowest since during this stage, the pupae were not influenced by food availability.

Inbreeding might also effect the fitness of mosquitoes including larval survivorship and mosquito longevity (Irvin et al., 2004; O'Donnell & Armbruster, 2010). Therefore, in this study, the inbreeding effect was avoided as much as possible, as mentioned in the first section of the experiment. The fitness of both strains was significantly different as determined from the demographic parameters generated from the jackknife $l_x m_x$ data for both strains. The SEL strain growth parameter was significantly higher than the KL strain (gross reproductive rate (*GRR*), the net reproductive rate (R_o), the intrinsic rate of

increase (r_m) and the finite rate of increase (λ). The mean generation times (T_c) and doubling times in days (T_d) were significantly lower for the SEL strain than the KL strain. This data also indicated that the SEL strain have a better life growth parameter than the KL strain mainly because it is more stable since it has been cultured in the laboratory longer than the KL strain. The other possible reason is the insecticide resistance status which might affect the fitness of the KL strain, since it was originally collected from dengue outbreak areas. In this study, the insecticide resistance status for this strain was not evaluated. It was reported that insecticide resistance such as to organophospate and pyrethroid negatively affected the fitness of *Ae. aegypti* including the development period, the fecundity and the survival rate of the mosquito (Belinato, Martins, & Valle, 2012; Martins et al., 2012; Diniz et al., 2015). It was also reported that the developmental period of permethrin resistant strain *Ae. albopictus* was longer than the susceptible strain (Chan & Zairi, 2013). Study by Bourguet et al. (2004) also indicated that organophosphate resistant strain *Culex pipiens* has a longer developmental time and shorter wing length than the susceptible strain.

Nevertheless, based on this data both strains showed capability of being established in the laboratory. The demographic parameters determined in this study can be compared with the study of *Ae. albopictus* life parameters in uncontrolled laboratory carried out by Nur Aida, et al. (2008b), with R_o value 68.70, r_m value 0.21, T_c value 10.55 and the study by Tsuda et al.(1994) which reported R_o value of 34.9/81.9, r_m value of 0.182/0.193, and T_c value of 26.1/30.0. These variations might be influenced by all factors affecting their survival and reproduction mentioned before such as geographical differences, culture parameters such as type of nutrition provided during immature or adult stages, physical environmental conditions such as the variability of temperature

and humidity, total number of generation/cohort used, competition and many more. Many studies on the life parameters of other mosquito species such as *Ae. aegypti* (Southwood et al., 1972; Lansdowne & Hacker, 1975; Costero et al., 1998; Irvin et al., 2004; Tejerina et al., 2009; Sowilem et al., 2013), *Culex* sp. (Walter & Hacker, 1974; Yao et al., 1988; Suman et al., 2011) and *Anopheles* sp.(Reisen & Mahmood, 1980; Maharaj, 2003; Okogun, 2005; Afrane et al., 2007; Olayemi & Ande, 2009) also recorded variations in the values of the life parameters with different factors affecting the life parameters. Data provided from this study can be used as a baseline data in order to understand more on the biology especially the life demographic of local strain *Ae. albopictus*.

ACKNOWLEDGEMENTS

We would like to thank the Director General of Health, Malaysia for his permission to publish this paper. We would also like to thank the Director of Institute for Medical Research and staff of Entomology Unit of Institute for Medical Research for their assistance and support in the study. This study was financially supported by the Ministry of Health Malaysia Grant; (NMRR -10-704-6570, JPP- IMR: 10-012)

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