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LIFE TABLE ESTIMATES FOR TWO COMMON *AEDES* MOSQUITO SPECIES: OBSERVATIONS FROM LARVAL HABITATS OF KOLKATA, INDIA

Sampa Banerjee[a], Dipanwita Das[b], Shreya Brahma[a], Soujita Pramanik[a], Goutam K. Saha[a] and Gautam Aditya[a]*

[a]Department of Zoology, University of Calcutta, 35 Ballygunge Circular Road, Kolkata 700019, India
[b]Department of Zoology, Bagnan College, Bagnan, Howrah 711303, India
*Corresponding author. Email: gautamaditya2001@gmail.com

Sampa Banerjee: https://orcid.org/0000-0001-9861-338X
Dipanwita Das: http://orcid.org/0000-0002-9875-7073
Shreya Brahma: https://orcid.org/0000-0001-5514-1474
Soujita Pramanik: https://orcid.org/0000-0002-5792-7689
Goutam K. Saha: https://orcid.org/0000-0002-9754-5458
Gautam Aditya: https://orcid.org/0000-0001-9445-879X

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Abstract. Life table features of dengue vectors are significant for the evaluation of the disease transmission potential. Using information on the larval stages thriving in different larval habitats in Kolkata, India, we evaluated life table features of *Aedes aegypti* (Linnaeus, 1762) and *A. albopictus* (Skuse, 1894) (Diptera: Culicidae). Daily monitoring of the larval habitats inhabited exclusively by either *A. aegypti* or *A. albopictus* was accomplished in order to estimate the instar-wise abundance and, based on it, the larval life table was constructed. Out of 90 positive larval habitats, ~34.4% was exclusively for *A. aegypti* and ~35.6% for *A. albopictus*. The life expectancy (e_x) of the instar I larva of *A. aegypti* and *A. albopictus* was 5 and 4 days, respectively. There was no significant difference found in survival of immature ($t_{(2),14} = 1.144$; $p = 0.272$) and adult ($t_{(2),6} = 0.536$; $p = 0.611$) individuals of the two species. Mortality of the immature stages of *A. aegypti* and *A. albopictus* was 82.14% and 96.15%, respectively. Lower values of the life expectancy of both *Aedes* species suggest faster larval development, as observed in other tropical and subtropical urban areas of the world.

INTRODUCTION

Dengue is an important mosquito-borne disease that is common in tropical and subtropical regions of the world and is rapidly spreading worldwide (WHO 2009). The number of dengue cases has increased from <0.5 million in 2010 to over 3.34 million in 2016 (WHO 2019). In India, irregular outbreaks of dengue fever have been reported during the last two centuries (Lall and Dhanda 1996; Gubler 1998), but the earliest virologically confirmed outbreak occurred in Vellore, Tamil Nadu, in 1956 (Rao 1987). The widespread distribution of dengue in tropical and subtropical regions is linked to the abundance of *Aedes aegypti* (Linnaeus, 1762) and *A. albopictus* (Skuse, 1894) (Diptera: Culicidae) (Christophers 1960; Gubler 1998), which coexist in larval habitats that are basically of container type (Braks et al. 2003, 2004; Juliano et al. 2004; Rey et al. 2006; Kamgang et al. 2010; Adeleke et al. 2013).

The biodemography of vector mosquitoes provides information on their life table features, which helps to integrate both life history strategies and vector management methods (Carey 2001; Okogun 2005; Ma and Bechinsky 2009; Aida et al. 2011). For successful management of vector mosquitoes, the biodemographic investigation of the concerned species is indispensable. Developmental times and survival rates of different life stages are most important in this respect. The life table serves as an important supplementary tool in framing mosquito control strategies, as it provides detailed analytical information about mortality, survival and life expectancy (Afrane et al. 2007; Carron et al. 2008; Hugo et al. 2014). Among the life table features, mortality between eggs and larval instars bears importance in reflecting the population build-up of both *A. aegypti* (Southwood et al. 1972; Service 1983; Focks et al. 1993a, b) and *A. albopictus* (Hashim et al. 2008). To be more precise, mortality of specific larval stages (3rd and 4th) of *A. albopictus* may predetermine the fate of the adult population build-up (Hashim et al. 2008).

The abundance of dengue vectors in urban areas of Kolkata, India reported in recent years (Banerjee et al. 2013a, b, 2015a, b), indicates the need for the estimation of life table parameters. Although Kolkata was the first city in India to document the dengue epidemic, the information available on dengue vectors is restricted to the estimation of their relative abundance in different time periods (Pramanik and Raut 2000, 2002; Pramanik et al. 2007; Banerjee et al. 2013a, b, 2015a, b). To reduce the incidence of dengue and abundance of *Aedes* mosquitoes, it is necessary to gain the information on their survivorship and larval development, as it would allow interpreting the life history patterns and successful completion of the life cycle. Interpretation of *Aedes* abundance can be used for more precise implementation of mosquito control strategies. Development of *Aedes* control strategies requires a broader understanding about its life cycle and life history. Nutritional resources available within the habitat determine the fate of the larval development of mosquitoes and related insects. In field habitats, different resource types can influence larval development and contribute to the differences in mosquito productivity and prospective population build-up (Banerjee et al. 2010, 2013a, b, 2015a, b). Therefore, for deepening the understanding of the population dynamics and the life history features of both *A. albopictus* and *A. aegypti* in Kolkata, studies on the life table of field collected immature stages are essential. The present study was undertaken with a view to provide the required information about survival as well as development rates of immature *A. aegypti* and *A. albopictus* encountered in container habitats.

MATERIALS AND METHODS

Immature stages of *A. aegypti* and *A. albopictus* were collected from in and around Ballygunge Science College Campus (22.5275° N, 88.3627° E), Kolkata, India, and adjacent localities, following Banerjee et al. (2010, 2013a, b) for three consecutive years, between 2014 and 2016, mainly during June–September. Primarily, the positive *Aedes* mosquito larval habitats were identified and immature stages (egg, larva and pupa) were collected. The habitat was continuously monitored for the following consecutive 15 days. If any habitat was found destroyed, it was excluded from the study. In our experiment, we employed the vertical life table method as samples were collected randomly, there were overlapping generations, and mosquito age distribution was stationary at the time of sampling (Edillo et al. 2004).

Immature mosquito stages (four larval stages and one pupal stage) were collected from positive artificial larval habitats, mainly earthen and plastic containers, into the specimen containers (with proper marking) (Tarson® India, 100 ml capacity) using either a hand net (mesh size 200 μm) or glass pipette fitted with a rubber tit or by pouring the entire contents of the larval habitat into a sampling bag (35.5 × 25.5 cm, 60 × 45 cm) depending on the water volume and abundance of immature mosquitoes encountered. In all instances, the habitat water was collected or tap water from the nearest source was considered to be the water source of the larval habitats. Addition of tap water or water from the same habitat did not affect the net-collected larvae, thereby justifying the mosquito immature transportation from the collected habitats to the laboratory. In the laboratory, the mosquito immature stages were emptied into enamel trays (39 × 23 × 4 cm size) separately, taking into consideration different larval habitats, and additional aged tap water was added when needed. Immature stages (larvae and pupae) of the mosquitoes collected from different larval habitats were counted instar-wise and recorded to construct the larval life table for both species.

To identify individual larval habitats exclusively for either *A. aegypti* or *A. albopictus* or for both species, individual immature mosquitoes were grown to adulthood. The larvae collected from each larval habitat were kept in their corresponding tray and were allowed to pupate using the nutritional resource present in the water collected from the field, i.e., no additional food was provided in the laboratory. Similarly, every pupa collected from the respective larval habitat was individually placed into a small glass vial (Borosil, India) (50 × 15 mm or 100 × 25 mm) with ~2 ml of water. The vials were covered with fine cloth and the pupae were allowed to emerge as adults. Upon eclosion of an adult, the mosquito was identified up to the species level following the identification keys (Reinert et al. 2004, 2009; Rueda 2004; WHO 2009; Rattanarithikul et al. 2010). Depending on the information on the eclosion and identity of the adult *Aedes* species, mosquito larval habitats exclusively for *A. aegypti* (31 larval habitats) and *A. albopictus* (32 larval habitats) were considered for the present study.

To construct the adult life table and to estimate adult survivorship, field collected instar III larvae were reared in the laboratory in six replicates, each with 50 individuals. Following pupation, the pupae were place in vials (15 mm × 50 mm) individually in 5 ml of distilled water and upon eclosion of adults, water was drawn from the vials with the help of a sterile syringe (Dispovan, India, 6 ml). The species of the adult was noted and the survival of adults after eclosion from pupae was recorded as adult longevity (in days). It was calculated by subtracting the day of eclosion from the day of individual's death and expressed in days. During this stage of the life cycle, the adults were not fed. Hence, their survival was solely dependent on the resources acquired during larval development.

Statistical analysis

To determine the instar duration of *A. aegypti* and *A. albopictus,* we conducted a mosquito rearing experiment. During the experiment, 49, 0-day old individuals of *A. aegypti* and 44, 0-day old individuals of *A. albopictus* were separately reared in 6-well plates with 10 ml water and *ad libitum* food resources, in the form of field collected detritus and fish food (Tokyu®, Malaysia). The instar duration of all larval and pupal stages of immature mosquitoes was recorded and the average value was considered for the present analysis. The dataset was used to deduce and plot the age distribution graph of the immature individuals of both species. Thus, the total numbers of immature mosquito individuals collected throughout the field survey were segregated into different stages (larval instars and pupae) and divided by the appropriate instar duration. The number/day values were plotted against the corresponding instar duration to obtain age distribution graphs following Service (1971). The number of individuals at the beginning of each instar was obtained from the regression equation, which was derived from number/day (y axis) and instar duration (x axis) separately for *A. aegypti* and *A. albopictus*. Life tables were constructed for immature and adult mosquitoes of both species (Service 1971; Southwood et al. 1972; Smith 1996; Southwood and Henderson 2000). For each species, a regression equation of age-specific survivorship was constructed using ln transformed data of l_x (survivorship) as a function of age (x, in days) (Reisen et al. 1979; Beier et al. 1987). Two sample *t*-tests (Zar 1999) were used to deduce any significant variations between the survival of immature and adult individuals of the two concerned mosquito species.

The survivorship and the life expectancy data were derived from the formula, where:

x = age interval or age class; N_x = number of survivors at the start of age interval x; l_x = proportion of organisms surviving to the start age interval x; d_x = proportion of the organisms dying during the age interval x to x + 1, $[l_x - (l_{x+1})]$; q_x = rate of mortality during the age interval x to x + 1, $[d_x/l_x]$; L_x = the average number of individuals alive during the age interval x to x + 1, $[(l_x + l_{x+1})/2]$; T_x = the total time period (in days) to be lived by individuals of age x in the population; e_x = the mean life expectancy of an individual alive at the start of the age interval x, $[T_x/l_x]$.

RESULTS

Our field survey identified 90 larval habitats positive for *Aedes,* out of which 31 larval habitats (~34.4%) were exclusively positive for *A. aegypti* and 32 larval habitats (~35.6%) were exclusively positive for *A. albopictus*. Also, the data of our field survey revealed that all five immature stages (four larval stages and one pupal stage) of mosquitoes were encountered during the random sampling of the selected study areas in Kolkata, India; of which the most abundantly represented was the instar IV larva of *A. aegypti* and the first instar I larva of *A. albopictus* (Figure 1). The instar duration of *A. aegypti* was found to be as follows: the instar I larva of *A. aegypti* – 1 day, the instar II larva – 1.08 days, the instar III larva –1.5 days, the instar IV larva – 3.02 days, duration of the pupa of this mosquito species being 1.98 days.

As for *A. albopictus,* duration of the instar I larva was 1.08 days that of the instar II larva – 1.23 days, the instar III larva – 1.82 days and the instar IV larva – 2.31 days, the pupa of this mosquito species lasting for 1.92 days (Figure 2). The age distribution graphs of both *A. aegypti* and *A. albopictus* slightly differed in shape, but the pattern was similar for both species of *Aedes*. The comparison of the respective instar duration between the

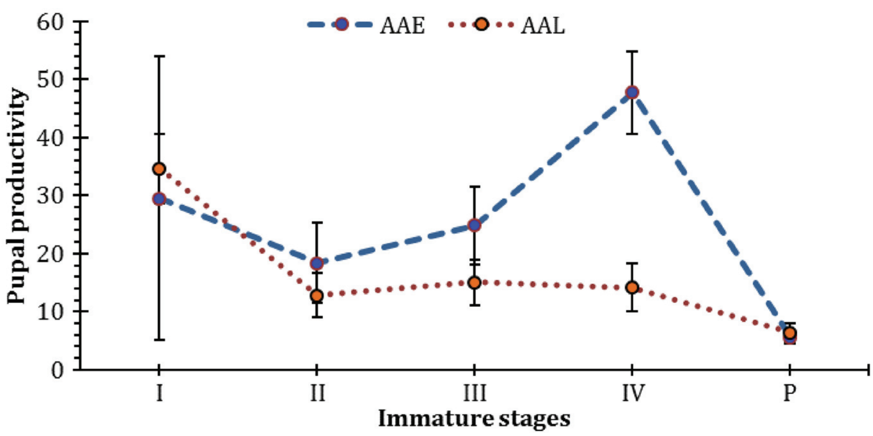

Figure 1. Productivity of the immature mosquito stages (mean ± SE) of the field-collected *Aedes* species, *A. aegypti* (AAE) and *A. albopictus* (AAL) from Kolkata, India, in sampling containers positive with the respective mosquitoes (n = 31, *A. aegypti*, n = 32, *A. albopictus*). Data on the total immature mosquito stages segregated into five different stages (larva and pupa) are presented in the graph.

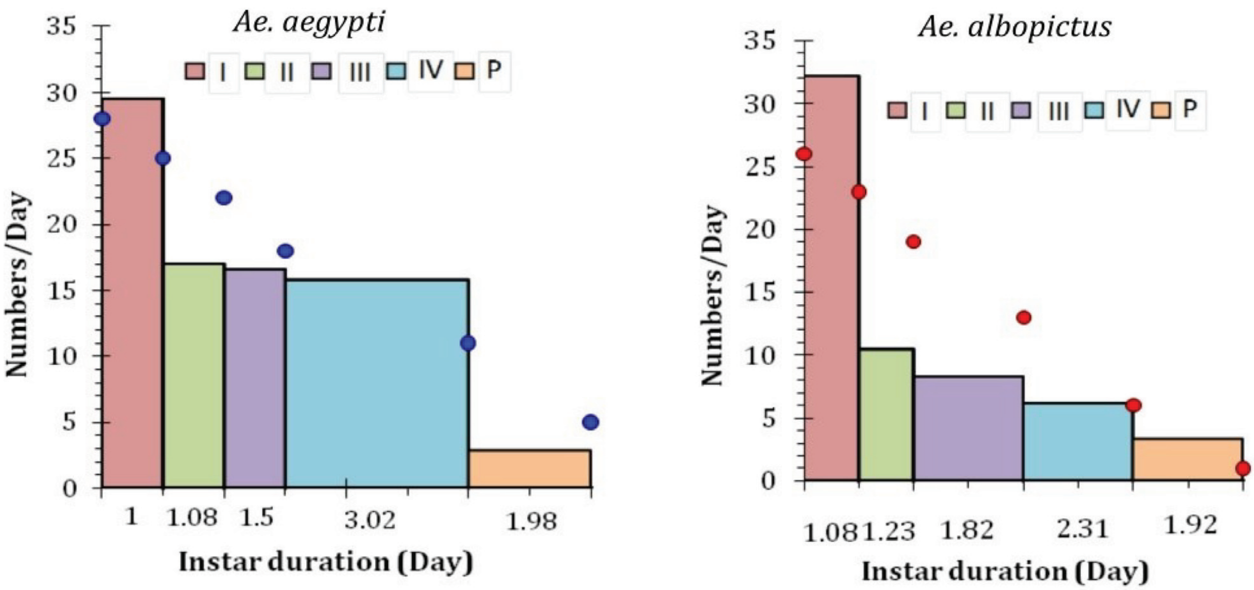

Figure 2. Age distribution of the immature stages of the field-collected *A. aegypti* and *A. albopictus*. The coloured round symbols represent numbers of individuals at the beginning of each instar.

Table 1. Life table data of the immature stages of the field-collected *Aedes* mosquitoes, (A) *A. aegypti* and (B) *A. albopictus* from Kolkata, India. The mean value of larvae from each habitat was considered for the analysis.
x = age interval or age class; N_x = number of survivors at the start of the age intervalx; l_X = proportion of organisms surviving to the start of the age interval x; d_x = proportion of the individuals dying during the age interval x to x + 1, $[l_x - (l_{x+1})]$; q_x = rate of mortality during the age interval x to x + 1, $[d_x/l_x]$; L_x = the average number of individuals alive during the age interval x to x + 1, $[(l_x + l_{x+1})/2]$; T_x = total time period (in days) to be lived by individuals of age x in the population; e_x = the mean life expectancy of an individual alive at the start of the age interval x, $[T_x/l_x]$.

(A) *A. aegypti*

Day (x)	No. of larva (N_x)	l_x	d_x	q_x	L_x	T_x	e_x
0	28	1	0.107	0.107	0.946	5.286	5.286
1	25	0.893	0.071	0.08	0.857	4.339	4.86
2	23	0.821	0.107	0.130	0.769	3.482	4.239
3	20	0.714	0.107	0.15	0.661	2.714	3.8
4	17	0.607	0.071	0.118	0.571	2.054	3.382
5	15	0.536	0.107	0.2	0.482	1.482	2.767
6	12	0.429	0.107	0.25	0.375	1	2.333
7	9	0.321	0.071	0.222	0.286	0.625	1.944
8	7	0.25	0.107	0.429	0.196	0.339	1.357
9	4	0.143	0.071	0.5	0.107	0.143	1
10	2	0.071	0.071	1	0.036	0.036	0.5
11	0	0	0	0	0	0	0

(B) *A. albopictus*

Day (x)	No. of larva (N_x)	l_x	d_x	q_x	L_x	T_x	e_x
0	26	1	0.115	0.115	0.942	4.192	4.192
1	23	0.885	0.115	0.130	0.827	3.25	3.673
2	20	0.769	0.115	0.15	0.712	2.423	3.15
3	17	0.654	0.115	0.177	0.597	1.712	2.618
4	14	0.539	0.153	0.286	0.462	1.115	2.071
5	10	0.385	0.115	0.3	0.327	0.654	1.7
6	7	0.269	0.115	0.429	0.211	0.327	1.214
7	4	0.154	0.115	0.75	0.096	0.115	0.75
8	1	0.039	0.039	1	0.019	0.019	0.5
9	0	0	0	0	0	0	0

Table 2. Life table estimates of the adult individuals that have emerged from pupae (reared from field-collected larvae) of (A) *A. aegypti* and (B) *A. albopictus* in six replicates each with 50 individuals for each replicate. Here the data of the newly emerged adults were considered.

(A) *A. aegypti*

Day (x)	No. of adult (N_x)	l_x	d_x	q_x	L_x	T_x	e_x
0	139	1	0	0	1	2.565	2.565
1	139	1	0.180	0.180	0.910	1.565	1.565
2	114	0.82	0.597	0.728	0.522	0.655	0.798
3	31	0.223	0.209	0.936	0.118	0.133	0.597
4	2	0.014	0.007	0.5	0.011	0.014	1
5	1	0.007	0.007	1	0.004	0.004	0.5
6	0	0	0		0	0	

(B) *A. albopictus*

Day (x)	No. of adult (N_x)	l_x	d_x	q_x	L_x	T_x	e_x
0	135	1	0.03	0.03	0.985	2.182	2.182
1	131	0.970	0.311	0.321	0.815	1.196	1.233
2	89	0.659	0.607	0.921	0.356	0.382	0.579
3	7	0.052	0.052	1	0.026	0.026	0.5
4	0	0	0		0	0	

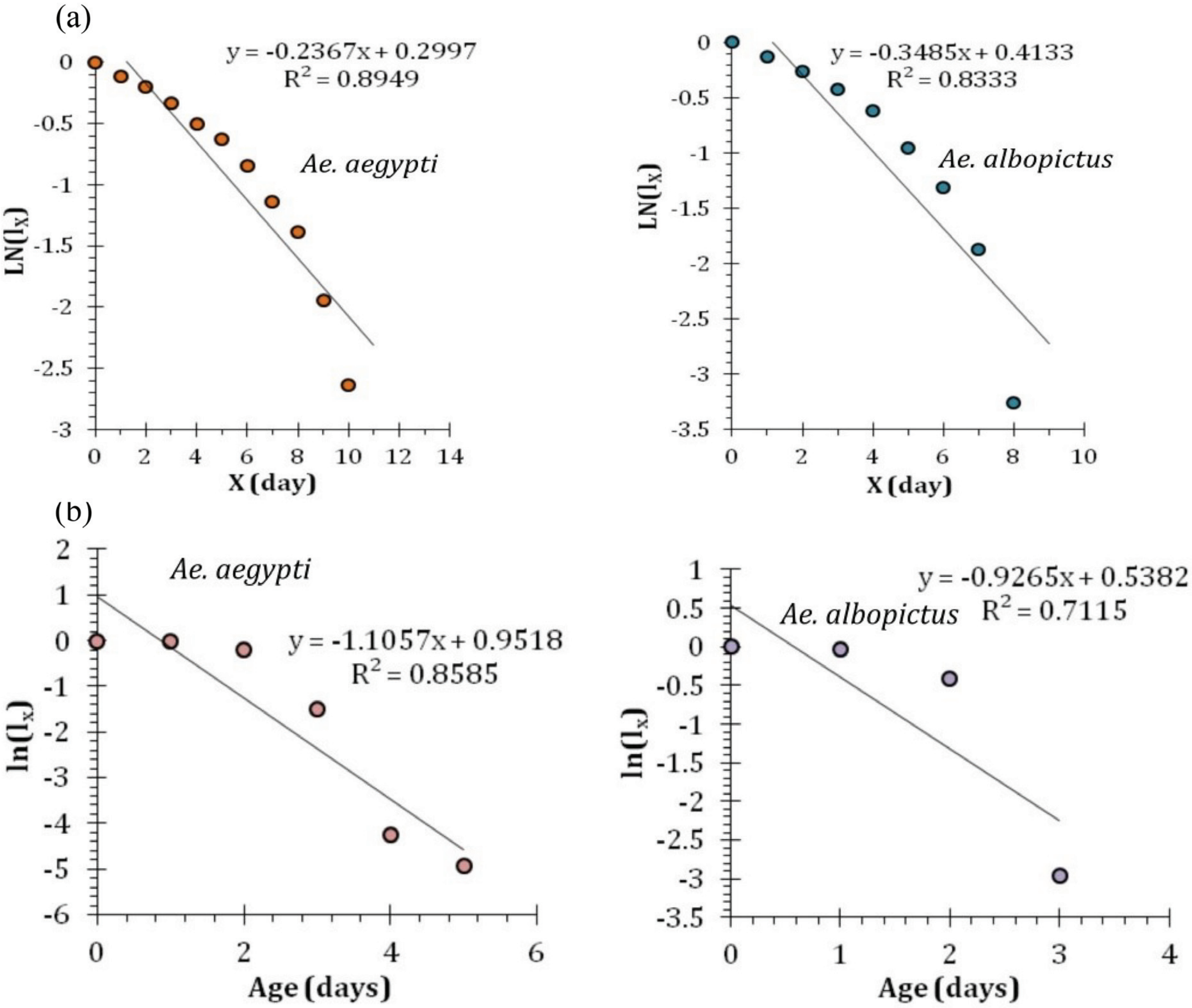

Figure 3 (a) Survivorship curves of the immature stages of the field-collected *Aedes* mosquitoes, *A. aegypti* and *A. albopictus* from Kolkata, India. The mean value of larvae from each habitat was considered for the analysis. (b) The survivorship curve of adult individuals (reared from field-collected larvae) of *A. aegypti* and *A. albopictus* in six replicates each with 50 individuals for each replicate.

Table 3. Instar mortalities of *A. aegypti* (A) and *A. albopictus* (B) during instar stages. *d = instar duration in days.

(A) *A. aegypti*

Instars/life stage	Age in days at the beginning of instars (t_{i-1})	No. of individuals entering instar stages ($S_{t_{i-1}}$)	Death during instar stages (D_i)	Relative proportion of individuals dying in instar stages $\left(\frac{D_i}{S_{t_{i-1}}}\right)$	Proportion of individuals dying daily in instar stages* $1-\left(\frac{S_{ti}}{S_{t_{i-1}}}\right)^{\frac{1}{d}}$
I	0	28	3	0.107	0. 07
II	1.00	25	3	0.12	0.111
III	2.08	22	4	0.182	0.125
IV	3.58	18	7	0.389	0.15
Pupae	6.60	11	6	0.545	0.329
Adults	8.58	5			

(B) *A. albopictus*

Instars/life stage	Age in days at the beginning of instars (t_{i-1})	No. of individuals entering instar stages ($S_{t_{i-1}}$)	Death during instar stages (D_i)	Relative proportion of individuals dying in instar stages $\left(\frac{D_i}{S_{t_{i-1}}}\right)$	Proportion of individuals dying daily in instar stages* $1-\left(\frac{S_{ti}}{S_{t_{i-1}}}\right)^{\frac{1}{d}}$
I	0	26	3	0.115	0.1074
II	1.08	23	4	0.174	0.112
III	2.31	19	6	0.316	0.188
IV	4.13	13	7	0.538	0.284
Pupae	6.44	6	5	0.833	0.607
Adults	8.36	1			

two species showed that in both species instar IV was the longest and instar I was the shortest (Figure 2).

The numbers of larvae (y) surviving to each age (x in day) were derived from two separate regression equations. For *A. aegypti*, the equation was y = -2.069× + 27.74, R^2 = 0.762 and that for *A. albopictus* was y = -3.095× + 25.90, R^2 = 0.633. The number of *A. aegypti* individuals at the beginning of each instar was found to be as follows: 28 at the beginning of the instar I larva, 25 – at the beginning of the instar II larva, 22 – at the beginning of the instar III larva, 18 – at the beginning of the instar IV larva, 11 – at the beginning of pupal stage, and 5 adult individuals. As for *A. albopictus*, the number of individuals at the beginning of the instar I larva was 26, at the beginning of the instar II larva – 23, 19 – at the beginning of the instar III larva, 13 at the start of instar IV larva, 6 at the beginning of the pupa, and 1 adult individual.

The survivorship and the life expectancy of the immature stages of both *Aedes* species are shown in Table 1 and Figure 3a. Our results indicate that life expectancy (e_x) of the 0-day old larval instar I of *A. aegypti* and *A. albopictus* were 5 and 4 days, respectively. There was no significant difference observed between surviving immature individuals of the two *Aedes* species ($t_{2,14}$ = 1.144; p = 0.272).

The survivorship curve and life table estimates for adult individuals are shown in Figure 3b and Table 2. Similarly, no significant difference was observed between adult survivors of the two concerned mosquito species ($t_{2,6}$= 0.536; p = 0.611). Mortality among the immature stages of *A. aegypti* and *A. albopictus* was 82.14% and 96.15%, respectively, which appears to be quite high, perhaps due to the habitat drying and resource shortage. The present study revealed that instar mortality was higher in *A. albopictus* and pupal mortality was higher in *A. aegypti* (Table 3).

DISCUSSION

According to the field data, productivity of *A. albopictus* was nearly equal to that of *A. aegypti* (Figure 1). Both the species coexist in urban environment, which increases the chances of dengue virus dispersal. The developmental time of vector mosquito immature is epidemiologically important. Rapid development signifies low parasitic infection, low predation, low risk from desiccation and large population with a chance of poorly developed pupae as larvae do not get enough time to accumulate sufficient amounts of nutrients (Aida et al. 2011). In the present study, the total time taken by instar I larvae of *A. aegypti* and *A. albopictus* to develop to the adult stage was 8.58 and 8.36 days (Figure 2), respectively. This result is supported by previous studies (Mahmood 1997; Tejerina et al. 2009; Maimusa et al. 2016). However, longer developmental times have also been reported in several cases (Christophers 1960; Beserra and Castro 2008; Olayemi and Ande 2009; Abu Kassim et al. 2012; Sowilem et al. 2013; Tripathi and Gupta 2018).

The comparison between mortality rates of the two populations of *A. aegypti* and *A. albopictus* revealed that in both species, mortality of the instar IV larva was highest, though pupal mortality was found to be higher in *A. aegypti* (Table 1 and Figure 3). Higher mortality of instar IV larva and pupa has been reported in several studies. Therefore, the life cycle-stage with the highest mortality rate is the key determinant phase in the mosquito population size (Mogi 1978; Reisen et al. 1989; Casanova and Do Prado 2002). Increased mortality of advanced stages of mosquito immature such as instar IV larva or pupa may be due to their relatively large body size, which makes them accessible for predators and other sources of mortality (Casanova and Do Prado 2002). In the present study, the percentage of the emerged *A. aegypti* and *A. albopictus* adults was 17.86 and 3.85, respectively. As observed earlier (Banerjee et al. 2010, 2013a, b, 2015b), the adult emergence of both the species may increase with higher abundance, and size and type of habitats. The mortality of the early instar stages was higher than that of the pupal stage (Table 3), which is characteristic of a typical type III survivorship curve (Deevey type III, Southwood and Henderson 2000). The life table data of field collected *A. aegypti* and *A. albopictus* immature observed in this study (Table 2 and Table 3) are comparable to those of *Anopheles culicifacies* and *A. stephensi* (Reisen et al. 1981), *A. sacharovi* (Yurttas and Alten 2007), *A. albimanus*, *A. vestitipennis* (Grieco et al. 2004), *Ochlerotatus albifasciatus* (Campos and Sy 2003), *A. gambiae* (Edillo et al. 2004), the predatory *Toxorhynchites rutilus* (Campos and Lounibos 2000) and *T. splendens* (Amalraj and Das 1996) and other mosquitoes from different parts of the world (Silver 2008). Survivorship and instar duration of *A. aegypti* differs from those of the above mentioned mosquito species due to species-specific adaptations and life history strategies, as well as due to the resource availability and physical condition in the larval habitats. If adults of both *A. aegypti* and *A. albopictus* do not get adequate food in time, they die early, which is probably because the newly emerged adults are solely dependent on the resources acquired during larval stages.

The ability to adapt to various food resources allows *Aedes* to thrive in varied habitat conditions. It has also been noted that food quality and amount influence the development of insects in general, including mosquitoes (Daugherty et al. 2000; Carey 2001; Dieng et al. 2002; Aditya et al. 2008, 2009; Juliano 2009). Larvae of *Aedes* mosquitoes tend to grow better in conditions of greater availability of nutritional resources, which varies with the nature of mosquito larval habitats. Larval growth, pupal productivity and mosquito population growth vary with the availability of food resources, which in turn is predetermined by the nature of the habitat (Bédhomme et al. 2003, 2005; Banerjee et al. 2010, 2013a, b; Mohan et al. 2014; Banerjee et al. 2015a, b). In view of the available information and observations made in the present study, it seems that together with climatic factors, habitat conditions, density of immature mosquito stages, and the availability of food resources can shape the larval development and population dynamics of *Aedes* mosquitoes The data obtained in this study may prove useful in formulating strategies for the population control of dengue vectors.

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Ethical Approval and consent to participate

Not applicable.

Consent for publication

All authors agree to publish the article in the present form

Contribution of the authors

Conceived by GA, SB and GKS; SB and DD carried out the field work with observations, collections and management of the immature of dengue vectors in laboratory; Data collection was performed by SB, DD and SP; Data analysis was performed by SB, GA, S Brahma; Drafting and compilation by SB and GA.

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Competing Interests

As authors of this article we declare no competing interest

Availability of data and materials

The data concerning observations of the present study can be shared upon authentic and reasonable request.

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