

**Research article**Submitted: August 30<sup>th</sup>, 2016 - Accepted: March 31<sup>st</sup>, 2017 - Published: June 30<sup>th</sup>, 2017**Effects of density dependent larval competition on the life history traits of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae)**Sampa BANERJEE<sup>1</sup>, Soujita PRAMANIK<sup>1</sup>, Soumyajit BANERJEE<sup>1,2</sup>, Goutam K. SAHA<sup>1</sup>, Gautam ADITYA<sup>1,\*</sup><sup>1</sup> Department of Zoology, University of Calcutta, 35 Ballygunge Circular Road, Kolkata 700019, India - 03banerjee.sampa@gmail.com; soujita.p@gmail.com; soumyajitb@gmail.com; gkszoo@gmail.com; gautamaditya2001@gmail.com<sup>2</sup> P.G. Department of Zoology, Serampore College, Serampore 712201, India

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**Abstract**

Consequences of larval competition at the population level provide explanation for the differences in relative abundance of *Aedes aegypti* and *Aedes albopictus* in different geographical regions. The outcome of competition is assessed through the estimates of the life history traits as a response to varying density and resource available for larval development. In the present study, variations in the life history traits due to density-dependent intra- and inter-specific competition involving *A. aegypti* and *A. albopictus* were assessed following the minimalist model. The instar-I larvae (0-day old F<sub>2</sub> generation) of both *Aedes* species were reared to the adult stages using the initial rearing density of 1, 2, 4 and 6 (individuals/10ml) in multiple replicates. The age at pupation, pupal weight, adult weight and adult wing length of the individuals were considered as the response variables and surrogates of estimating the competitive interactions. Density dependent variations in the competitive interactions were evident for both the mosquitoes with reference to the selected life history traits. In *A. aegypti*, the life history traits varied with the levels of competition, which was not observed for *A. albopictus*. Although the density levels considered in the present instance were lower than in earlier studies, the observations were similar, with *A. albopictus* being competitively superior. It appears that irrespective of the density levels, interspecific competition affects *A. aegypti* and thus may bear population level consequences and overall abundance in the areas where both species are present.

**Keywords:** Larval competition, dengue, *Aedes* mosquitoes, life history traits.**Introduction**

The dengue vectors *Aedes aegypti* (Linnaeus, 1762) and *Aedes albopictus* (Skuse, 1894) (Diptera: Culicidae) co-exist in the larval habitats in almost all tropical regions of the world (O'Meara et al. 1995; Braks et al. 2003, 2004; Juliano et al. 2004; Rey et al. 2006; Kamgang et al. 2010; Adeleke et al. 2013; Banerjee et al. 2013 a, b). Owing to the similarities in the life history strategies and general biology, both *A. aegypti* and *A. albopictus* tend to exploit similar resources, which may lead to competitive interactions (Juliano 2009). As a consequence of the competitive interactions, variations in the life history traits are observed that affect the fitness of individual mosquito and the population as well. Recent studies indicate that the disease transmission potential of *Aedes* mosquitoes is linked with the fitness of the individuals as indicated through the life history traits like the pupal weight and adult body weight (Alto et al. 2005, 2008a, b, 2015; Reiskind & Lounibos 2009). Use of the life history traits as surrogate of fitness of mosquitoes enables understanding the links between the

ecological factors and the disease transmission potential. Considering the smaller containers as the larval habitats of dengue vectors, the resource availability and the habitat permanence appears to be the key factors influencing the larval development and the extent of fitness of individual mosquito (Strickman & Kittayapong 2003; Arrivillaga & Barrera 2004; Banerjee et al. 2013b, 2015b). Resources inside the larval habitats are supposedly limited, due to smaller size, which act as a limiting factor for the developing larva (Bradshaw & Holzapfel 1992; Renshaw et al. 1994). Empirical evidences have shown that both intraspecific and interspecific competitions involving the two mosquito species, under resource limitation (Daugherty et al. 2000; Yee et al. 2004; Murrell et al. 2011) or temperature variations (Lounibos et al. 2002; Westbrook et al. 2010; Couret et al. 2014), influence the life history traits. The outcome of larval competition involving *A. aegypti* and *A. albopictus*, varies with the quality and quantity of resource available in the larval habitats, and is aptly defined as 'context dependent' (Juliano 2009). In addition to the resource quality and quantity, the relative density of the

developing larvae can be a factor in determining the fitness of the adult mosquitoes (Agnew et al. 2002; Bédhomme et al. 2003; Arrivillaga & Barrera 2004).

The density of the developing larvae within the space concerned is a critical factor influencing the pace of development and fitness of the individual mosquito (Broadie & Bradshaw 1991; Renshaw et al. 1994; Lord 1998; Reiskind & Lounibos 2009). Differences in the density of the developing individuals under similar space and resource condition would mean differences in the per capita resource availability and thus affecting the developmental pace and biomass accumulation in the individual mosquito. Density dependent effects on the mosquito larvae have been evaluated using rearing densities of higher magnitude ranging between 10 and 320 (Daugherty et al. 2000; Braks et al. 2004; Leishnam & Juliano 2010; Gilles et al. 2011) excepting in few instances where the minimalist approach is adopted using densities of much lower magnitude (Agnew et al. 2000, 2002; Bédhomme et al. 2003). Using the minimalist approach the variations in the life history traits at the individual levels can be deciphered with a higher precision due to calibration of the individual density at lower magnitude of 2, 3 or 4 individuals/ 10ml, against single individual as a control. Such density dependent effects on the fitness of the mosquitoes have been demonstrated for the mosquitoes like *Culex quinquefasciatus* (Agnew et al. 2000), *Aedes aegypti* (Agnew et al. 2002) and *Anopheles stephensi* (Grech et al. 2007). The manipulation of the rearing density to the minimum enables deciphering the sex based differences of the density-dependent competition (Agnew et al. 2000, 2002). In the present study an effort is being made to decipher the effects of the intra- and inter-specific competition following the minimalist form of rearing density using *A. aegypti* and *A. albopictus*. Although earlier studies have demonstrated the effects of the intraspecific and interspecific interactions involving these two mosquitoes (Daugherty et al. 2000; Juliano 2009; Reiskind & Lounibos 2009), the density of the interacting individuals were comparatively higher than what is being proposed here. The results of the present study will enable deducing the extent of competition of the two species at substantially low density levels.

## Materials and methods

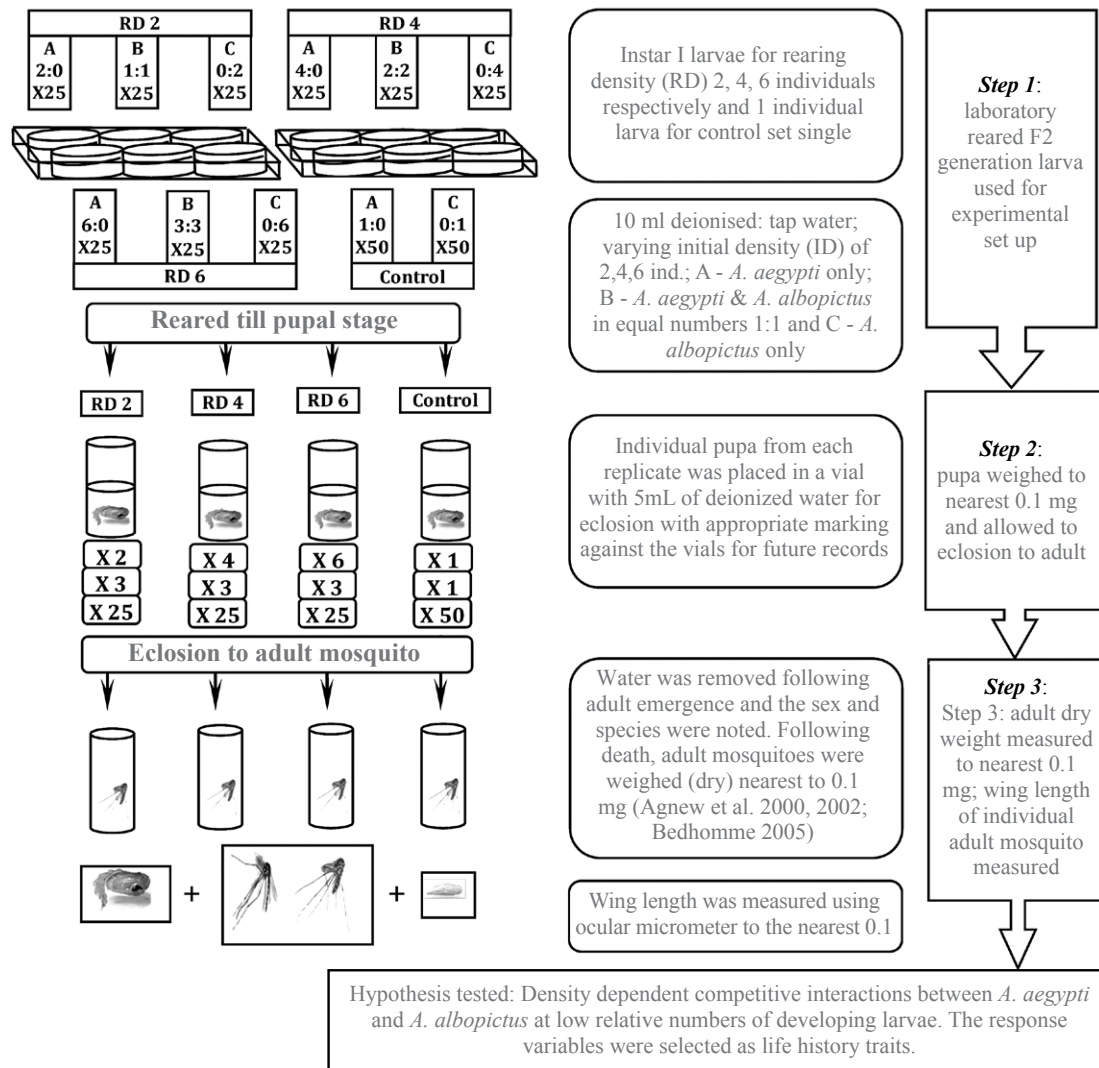
### Laboratory rearing and Experimental design

Immature stages of both the mosquito species *A. aegypti* and *A. albopictus* were collected from different larval habitats of selected sites of urban and suburban areas of Kolkata, India following standard sampling protocol with required modifications (Banerjee et al. 2013a, b; 2015a, b). Considering the field collected immature as P- generation, the mosquitoes *A. aegypti* and *A. albopictus* were reared in the laboratory, separately. The eggs from F<sub>2</sub>-generation of both species were hatched synchronously and 0-day old (<

6 h) instar I larvae were transferred to the 6-well culture plates (Tarson®, India), considering each well as a single replicate, containing 10 ml deionised water to initiate the experiment. To assess the competitive effect on the life history traits of these two mosquito species two levels of competitive interaction were considered - i) intraspecific competition, where only a single species compete for the food and space, ii) interspecific competition, where both species in a ratio of 1:1, compete with each other for food and space. In order to achieve this, the initial rearing densities - two, four, and six individuals per container, were kept constant but the species combinations were varied according to type of competitions. Also, one individual per well of each species was set as control. In all the experimental wells, the larvae were provided with fish food (Tokyu®, Japan), *ad libitum*. These eight treatments (4 densities, 2 competitive interactions) for each mosquito species were repeated at least 25 times. Proper monitoring was carried out for the rearing of the larvae in the laboratory with the temperature and relative humidity being  $27 \pm 2^\circ\text{C}$  and  $70 \pm 2\%$ , respectively. At the end of 24 h period, the water was changed and fresh grain of food was added in the wells of plates. The wells of the culture plates were monitored daily for pupation. Upon pupation the date of pupation was recorded (AP – Age at Pupation) and individual pupa were weighed (PW – Pupal Weight) up to the nearest 0.1 mg using pan balance (ADAM®, ADA 71/L, Adam Equipment, UK). This was followed by placement of the pupa in glass vial (15 X 50mm) containing 5 ml of double distilled water and then the vials were covered with fine cloth and allowed for eclosion. The vials were numbered serially against the date of pupation under respective initial density and levels of competition. Following eclosion, the water from the vials was removed using a sterile syringe and the sex (for both intraspecific and interspecific competition) and species (for interspecific competition) of the adult were noted and recorded. After natural death of the mosquitoes, the adult dry weight (AW – Adult Weight) was recorded nearest to 0.1 mg and then one wing were taken off from each individual and length was measured to the nearest 0.1 mm using a dissecting stereo microscope (Olympus® SZX, Olympus Corporation, Tokyo, Japan) fitted with a graduated eyepiece (Erma®, Japan). The experimental design for the present study is outlined in Fig. 1.

### Statistical Analysis

To assess the effect of varying density and different levels of competitive interaction on various life history traits of two mosquito species *A. aegypti* and *A. albopictus* the data obtained were subjected to three-way ANOVA, where three density levels (initial density 2, 4 and 6 individuals/10ml), two competitive interactions (inter- and intra-specific) and sexes (male and female) of the concerned mosquito species were considered as explanatory variables. The life history traits like age at pupation (AP



**Fig. 1** – The experimental protocol followed in the present study emphasizing the replicates used for the rearing density of the mosquitoes.

in days), pupal weight (PW in mg), adult weight (AW in mg), wing length (WL in mm) were considered as the dependent variables.

In order to assess the density effects on the life history traits of the two mosquito species, a comparison with the reference value was made (rearing density of 1 individual was considered as reference for no competition) employing the formula:

$$\text{Density Impact (DI)} = \frac{(\text{LHT}_{\text{ID}} - \text{LHT}_{\text{C}})}{[(\text{LHT}_{\text{ID}} + \text{LHT}_{\text{C}})/2]}$$

where  $\text{LHT}_{\text{ID}}$  = The life history trait of an individual reared under a particular initial density;  $\text{LHT}_{\text{C}}$  = The life history trait of an individual of control set. The formula employs the difference in the values for the life history trait between the treatment and control rearing densities, identical to the format of degree of sexual dimorphism (Sharmila Bharati et al. 2004). The data obtained for each

density and sex levels for the DI using the formula mentioned above, were subjected to logistic regression following generalized linear model with logit link. In this study the dependent variables or the response variables ( $\text{DI}_{\text{AP}}$  - Density impact on age at pupation,  $\text{DI}_{\text{PW}}$  - Density impact on pupal weight,  $\text{DI}_{\text{WL}}$  - Density impact on wing length) follows binomial (n, p) distribution with n replicates for each explanatory variables (the levels of the explanatory variables are density- 3, level of competition-2, sex- 2). In this instance, the probability parameter p was regarded as the linear combination of explanatory variables (density, competition and sex). A binary function with logit link was employed to relate the probability (p) with the explanatory variables and the parameters were estimated through maximum likelihood using the software XLSTAT (Addinsoft 2010). The density impact (DI) on the life history traits was expressed through the logistic regression of the form:  $(y) = 1/(1 + \exp(- (a + b_1x_1 - b_2x_2 - b_3x_3)))$ , where

$x_1$  is competition types,  $x_2$  is density,  $x_3$  is sex. The parameter estimates of the explanatory variables were judged through a Chi square value (Wald's Chi-square) for the significant contribution in the variations in the values observed. The statistical analyses were performed following Zar (1999).

## Results

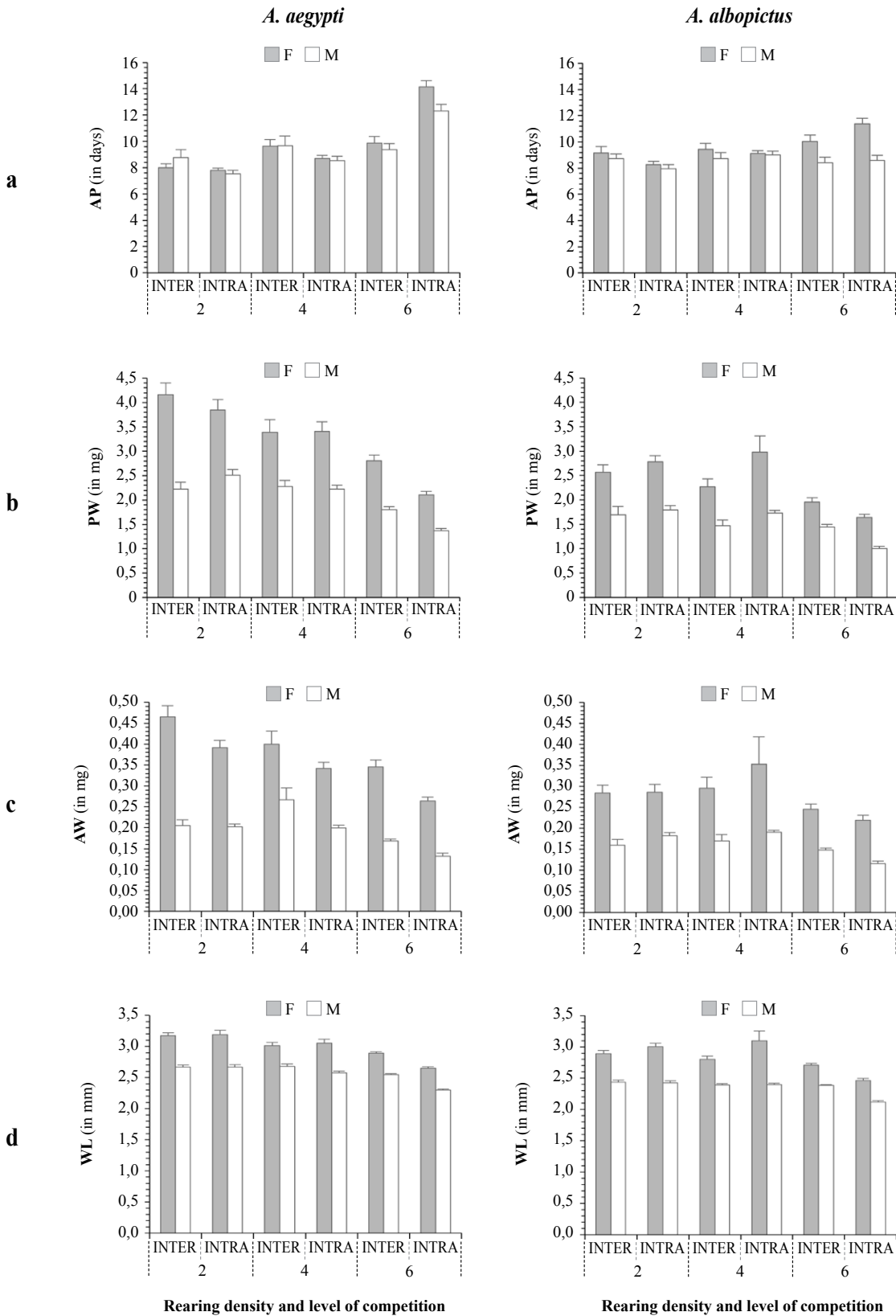
The effects of the density and the type of competition on the life history traits were observed for *A. aegypti* while only the density effects was observed for *A. albopictus*. Sex specific differences to the life history traits were observed in both the mosquitoes. As shown in Fig. 2, the age at pupation was extended and the pupal weight, adult weight and the wing length exhibited a declining trend with reference to the density in both species. Irrespective of the density and mode of competitive interactions when compared among two sexes of *A. aegypti* it was evident that females were larger in terms of pupal weight, adult weight and wing length than that of their male counterparts. Though the variation was not much profound for age at pupation, but females of *A. aegypti* took more time than the males for pupation (Fig. 2). Similar pattern were observed for *A. albopictus* also, where the females were greater than the males in terms of size (Fig. 2). The age at pupation of female *A. albopictus* were higher than their male counterparts and unlike *A. aegypti* the variation in age at pupation for females and males of *A. albopictus* were highly significant (Table 1). The results of the 3-way ANOVA (Table 1) revealed density, level of competition and sex being significant contributors for the variations observed in the life history traits of *A. aegypti*. Similar results were observed for *A. albopictus* except that the levels of competition did not bear any consequence on the life history traits (Table 1).

When reared as single, the females of *A. aegypti* took on an average  $7.11 \pm 0.11$  S.E. days (range 7.00 – 8.00 days) to reach pupal stage with an average weight of  $3.22 \pm 0.19$  S.E. mg (range 1.90 – 4.00 mg), and eclosed to adult of an average  $0.42 \pm 0.03$  S.E. mg (range 0.23 – 0.53 mg) body weight with corresponding wing length of mean  $3.00 \pm 0.06$  S.E. mm (range 2.59 – 3.24 mm). In comparison, for the males of *A. aegypti*, the mean age at pupation was  $6.93 \pm 0.12$  S.E. days (range 6.00 – 8.00 days), while the mean pupal weight was  $2.35 \pm 0.05$  S.E. mg (range 2.10 – 2.80 mg). The corresponding mean adult weight was  $0.29 \pm 0.01$  S.E. mg (range 0.25 – 0.36 mg) and the mean wing length was  $2.62 \pm 0.02$  S.E. mm (range 2.54 – 2.76 mm), considerably less than the females. For *A. albopictus* females, the age at pupation were on an average  $8.00 \pm 0.11$  S.E. days (range 7.00 – 9.00 days), mean pupal weight was  $2.68 \pm 0.08$  S.E. mg (range 1.90 – 3.20 mg), mean adult weight was  $0.41 \pm 0.02$  S.E. mg (range 0.27 – 0.51 mg) and mean wing length was  $2.95 \pm 0.04$

S.E. mm (range 2.59 – 3.20 mm), when reared as single individual. The males of *A. albopictus* reared as single individual achieved pupation on an average  $7.45 \pm 0.16$  S.E. days (range 7.00 – 8.00 days), with a mean pupal weight of  $2.68 \pm 0.08$  S.E. mg (1.20 – 1.90 days), mean adult weight as  $0.19 \pm 0.01$  S.E. mg (range 0.14 – 0.21 mg) and mean wing length of  $2.38 \pm 0.03$  S.E. mm (range 2.19 – 2.46 mm). When the life history traits of other individuals were compared to the control set (initial rearing density of one individual), the density effect on the different life history traits was evident, for both sexes. Using the DI as the indicator of the effects of density, it was observed that for both species, the density impact was profound for all the life history traits. For both *A. aegypti* and *A. albopictus* pupation was delayed as density increased and age at pupation was highest for both the sexes when six conspecific individuals were in competition (Fig. 3a). Irrespective of the mode of competitive interactions, for males and females of *A. aegypti* pupal weight reduced only when six individuals compete with each other whereas for females and males of *A. albopictus* pupal weight was decreased as number of competitor increased in the rearing habitats irrespective of level of competitive interaction (Fig. 3b). Adult body weight also decreased as the rearing density increased for both the concerned species irrespective of two sexes (Fig. 3c). The wing length of both species and sexes reduced with the increase in density (Fig. 3d). The application of the logistic regression on the values of the density impact reflects that for *A. aegypti* the effects were more prominent than the other species in context. For *A. aegypti* the results of the logistic GLM (Table 2) indicated significant effects of density on age at pupation ( $DI_{AP}$ ), pupal weight ( $DI_{PW}$ ), adult weight ( $DI_{AW}$ ) and wing length ( $DI_{WL}$ ).

## Discussion

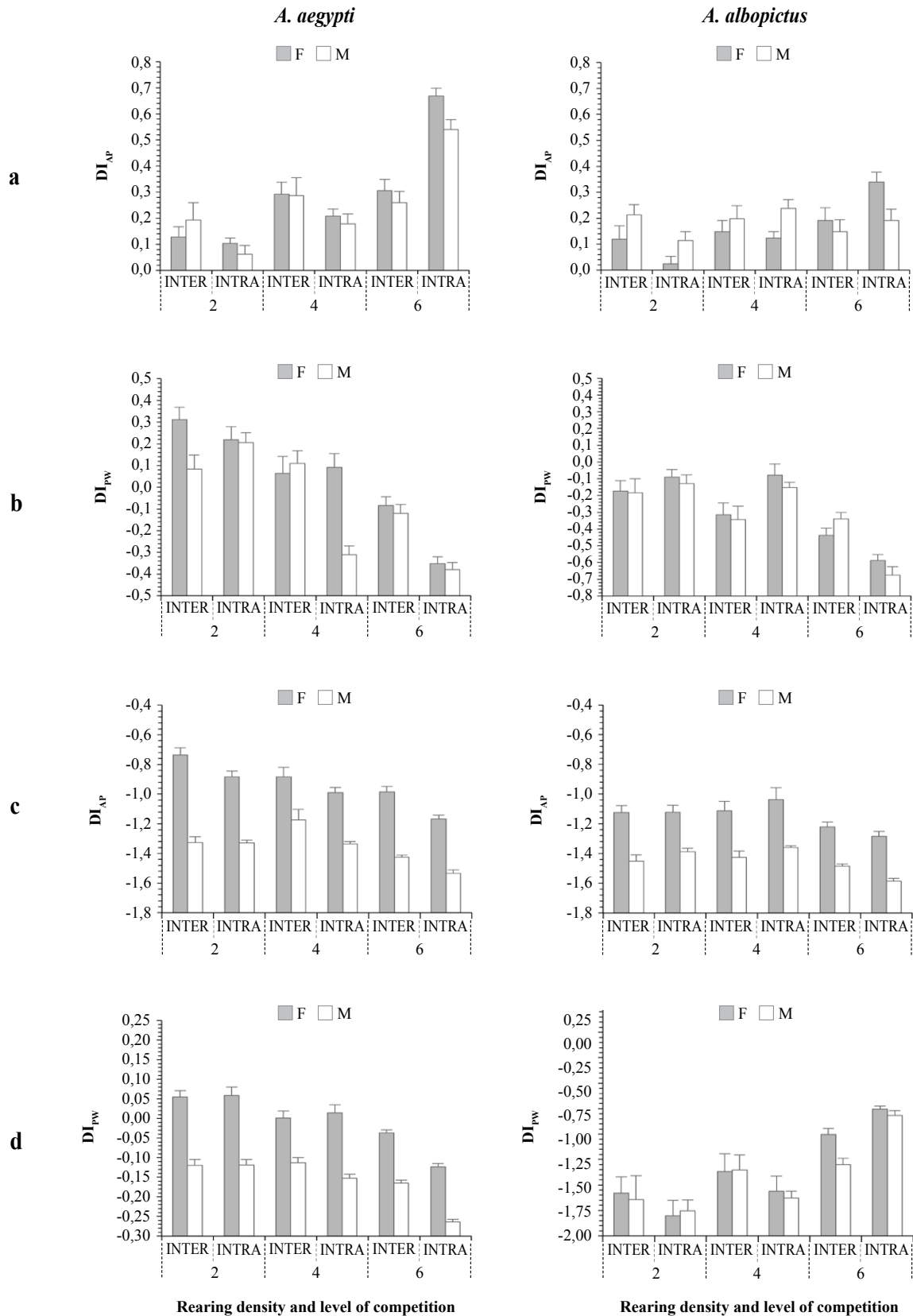
The density dependent effects on the life history traits have been recorded for different mosquito species including *A. aegypti* and *A. albopictus* (Agnew et al. 2002; Bédhomme et al. 2003; Arrivillaga & Barrera 2004; Legros et al. 2009; Reiskind & Lounibos 2009; Alto et al. 2015). Rearing density of the developing larvae is critical, since it determines the *per capita* availability of the resources which in turn is the primary factor affecting the developmental pace and the expression of the life history traits. In majority experiments, the alteration in the rearing density influenced the larval development and the body size of mosquitoes, thereby affecting the fitness components (Braks et al. 2004; Alto et al. 2005, 2008a, b; Reiskind and Lounibos 2009). In such experiments with density treatments, the initial rearing densities of the larvae are quite high, ranging between 20 and 320 individuals (Daugherty et al. 2000; Braks et al. 2004; Alto et al. 2008a; Leisnham & Juliano 2010). In contrast, the present observations were made at a much lower scale following the norms of the minimalist ap-



**Fig. 2** – The variations (mean  $\pm$  SE) in the life history traits of the two mosquitoes *A. aegypti* and *A. albopictus* under intra- and interspecific competitions in minimalist form of density of the individuals in the rearing containers. In all instances at least 20 replicates were considered for all the levels of density shown in the x-axis. Shaded bars represent ♀ while non-shaded bars represent ♂. The life history traits considered are (a) age at pupation (AP in days), (b) pupal weight (PW, in mg), (c) adult dry weight (AW, in mg) and (d) adult wing length (WL, in mm).

**Table 1** – The results of the three way ANOVA using the density, sex and competition levels as source of variations for the response variables (life history traits). The F-values marked in bold are significant at  $p < 0.001$  level. Here the explanatory variables are Level of competition, density levels and sex of the species and the response variables are - AP (age at pupation in days), PW (pupal weight in mg), AW (adult weight in mg) and WL (wing length in mm).

<i>A. aegypti</i>					<i>A. albopictus</i>				
Source	SS	DF	MS	F	Source	SS	DF	MS	F
<i>Age at Pupation (AP in days)</i>					<i>Age at Pupation (AP in days)</i>				
Competition	16.396	1	16.396	<b>4.548</b>	Competition	0.041	1	0.041	0.014
Density	335.969	2	167.984	<b>46.599</b>	Density	30.676	2	15.338	<b>5.112</b>
Sex	4.652	1	4.652	1.291	Sex	44.119	1	44.119	<b>14.705</b>
Competition*Density	205.210	2	102.605	<b>28.463</b>	Competition*Density	17.499	2	8.750	2.916
Competition*Sex	7.908	1	7.908	2.194	Competition*Sex	0.210	1	0.210	0.070
Density*Sex	15.408	2	7.704	2.137	Density*Sex	32.917	2	16.458	<b>5.486</b>
Competition*Density*Sex	2.712	2	1.356	0.376	Competition*Density*Sex	6.856	2	3.428	1.143
Error	674.117	187	3.605		Error	567.061	189	3.000	
<b>Total</b>	<b>1175.120</b>	<b>198</b>			<b>Total</b>	<b>703.430</b>	<b>200</b>		
<i>Pupal Weight (PW in mg)</i>					<i>Pupal Weight (PW in mg)</i>				
Competition	1.694	1	1.694	<b>4.222</b>	Competition	0.346	1	0.346	0.822
Density	39.815	2	19.907	<b>49.625</b>	Density	16.856	2	8.428	<b>20.032</b>
Sex	64.247	1	64.247	<b>160.153</b>	Sex	31.158	1	31.158	<b>74.054</b>
Competition*Density	3.057	2	1.528	<b>3.810</b>	Competition*Density	6.188	2	3.094	<b>7.353</b>
Competition*Sex	0.742	1	0.742	1.849	Competition*Sex	0.594	1	0.594	1.411
Density*Sex	3.904	2	1.952	<b>4.866</b>	Density*Sex	1.743	2	0.871	2.071
Competition*Density*Sex	0.773	2	0.387	0.964	Competition*Density*Sex	0.288	2	0.144	0.343
Error	75.017	187	0.401		Error	79.521	189	0.421	
<b>Total</b>	<b>184.619</b>	<b>198</b>			<b>Total</b>	<b>143.015</b>	<b>200</b>		
<i>Adult Weight (AW in mg)</i>					<i>Adult Weight (AW in mg)</i>				
Competition	0.122	1	0.122	<b>25.572</b>	Competition	0.002	1	0.002	0.177
Density	0.264	2	0.132	<b>27.530</b>	Density	0.163	2	0.081	<b>6.126</b>
Sex	1.278	1	1.278	<b>266.975</b>	Sex	0.618	1	0.618	<b>46.464</b>
Competition*Density	0.005	2	0.002	0.507	Competition*Density	0.038	2	0.019	1.432
Competition*Sex	0.014	1	0.014	2.918	Competition*Sex	0.001	1	0.001	0.048
Density*Sex	0.057	2	0.028	<b>5.910</b>	Density*Sex	0.016	2	0.008	0.603
Competition*Density*Sex	0.013	2	0.006	1.307	Competition*Density*Sex	0.006	2	0.003	0.223
Error	0.895	187	0.005		Error	2.514	189	0.013	
<b>Total</b>	<b>2.675</b>	<b>198</b>			<b>Total</b>	<b>3.485</b>	<b>200</b>		
<i>Wing Length (WL in mm)</i>					<i>Wing Length (WL in mm)</i>				
Competition	0.326	1	0.326	<b>11.388</b>	Competition	0.018	1	0.018	0.234
Density	3.194	2	1.597	<b>55.812</b>	Density	2.716	2	1.358	<b>17.995</b>
Sex	7.732	1	7.732	<b>270.198</b>	Sex	9.589	1	9.589	<b>127.051</b>
Competition*Density	0.544	2	0.272	<b>9.503</b>	Competition*Density	1.422	2	0.711	<b>9.418</b>
Competition*Sex	0.034	1	0.034	1.200	Competition*Sex	0.224	1	0.224	2.967
Density*Sex	0.185	2	0.093	<b>3.234</b>	Density*Sex	0.436	2	0.218	2.889
Competition*Density*Sex	0.051	2	0.026	0.899	Competition*Density*Sex	0.142	2	0.071	0.938
Error	5.352	187	0.029		Error	14.264	189	0.075	
<b>Total</b>	<b>17.577</b>	<b>198</b>			<b>Total</b>	<b>30.385</b>	<b>200</b>		



**Fig. 3** – The variations (Mean ± SE) of density impact (DI) on different life history traits (AP- age at pupation, PW- pupal weight, WL- wing length) of two mosquito species under intra- and inter- specific competitions. Shaded bars represent ♀ while non-shaded bars represent ♂. The life history traits are shown in sequence as (a) Age at pupation, (b) pupal weight, (c) adult weight and (d) wing length. Values less than zero indicates density impact.

**Table 2** – The results of the binomial GLM with logit link to test the effects of the competition, density and sex (explanatory variables) on the density impact of the selected life history traits (response variable). The values in bold represent significance at  $P < 0.05$  level.

<i>A. aegypti</i>					<i>A. albopictus</i>				
	Intercept	Competition	Density	Sex		Intercept	Competition	Density	Sex
<b>DI<sub>AP</sub></b>					<b>DI<sub>AP</sub></b>				
Value	1.09	-0.25	<b>2.07</b>	<b>-1.60</b>	Value	0.164	0.087	0.218	0.361
SE	1.31	0.48	0.40	0.50	SE	0.822	0.349	0.189	0.339
Wald $\chi^2$	0.69	0.27	27.10	10.19	Wald $\chi^2$	0.040	0.062	1.326	1.136
Pr > $\chi^2$	0.41	0.60	< 0.0001	0.00	Pr > $\chi^2$	0.842	0.803	0.250	0.286
<b>DI<sub>PW</sub></b>					<b>DI<sub>PW</sub></b>				
Value	6.22	<b>-1.10</b>	<b>-1.63</b>	<b>-0.93</b>	Value	-0.156	0.765	<b>-1.621</b>	-0.680
SE	1.13	0.37	0.26	0.34	SE	1.313	0.500	0.709	0.471
Wald $\chi^2$	30.38	8.59	40.72	7.35	Wald $\chi^2$	0.014	2.346	5.234	2.087
Pr > $\chi^2$	< 0.0001	0.00	< 0.0001	0.01	Pr > $\chi^2$	0.906	0.126	0.022	0.149
<b>DI<sub>AW</sub></b>					<b>DI<sub>AW</sub></b>				
Value	-10.079	<b>1.563</b>	<b>1.365</b>	<b>4.437</b>	Value	-4.364	0.318	<b>0.868</b>	3.926
SE	1.733	0.486	0.330	0.688	SE	1.750	0.500	0.358	1.414
Wald $\chi^2$	33.826	10.334	17.131	41.589	Wald $\chi^2$	6.221	0.403	5.876	7.709
Pr > $\chi^2$	< 0.0001	0.001	< 0.0001	< 0.0001	Pr > $\chi^2$	0.013	0.525	0.015	0.005
<b>DI<sub>WL</sub></b>					<b>DI<sub>WL</sub></b>				
Value	8.41	-0.06	<b>-1.71</b>	<b>-4.89</b>	Value	-8.649	-0.592	<b>4.532</b>	0.112
SE	1.70	0.48	0.36	0.91	SE	3.364	1.448	0.720	1.441
Wald $\chi^2$	24.55	0.02	22.17	28.93	Wald $\chi^2$	6.612	0.167	39.628	0.006
Pr > $\chi^2$	< 0.0001	0.90	< 0.0001	< 0.0001	Pr > $\chi^2$	0.010	0.683	< 0.0001	0.938

proach. However, the effects of the density dependent intraspecific competition employing minimalist approach remained similar to the high density treatments. Use of low number of individuals in treatments enables inclusion of considerable number of replicates to judge the consistency of the results. A comparison with the control is also achievable in the minimalist approach such that the effects of the deviations from the optimal values can be deduced. The relative density of the larvae in the mosquito larval habitats varies with the size of the habitat (Sunahara et al. 2002), observed in Kolkata, India (Banerjee et al. 2010) and adjoining areas (Aditya et al. 2008, 2009). The diversity of the larval habitats exploited by the *Aedes* mosquitoes and the pupal productivity observed therein (Banerjee et al. 2013a, 2015a, b) suggests considerable variations in the relative number of developing larvae in the larval habitats at any instance. Particularly, in the smaller container habitats originating from the disposed household wastes, the number of larvae may correspond to the numbers used in the present treatments, justifying the employment of the minimalist approach.

The rearing density of the larva bears a direct conse-

quence to the developmental time, pupal weight, adult weight and longevity in all instances where the competitive interactions have been evaluated. Similar observation was found in the present study for both species as rearing density increased from single individual to six individuals, the life history traits got affected which support the previous work employing minimalist approach (Agnew et al. 2000, 2002). In each treatment, irrespective of the levels of competition, for both *A. aegypti* and *A. albopictus*, the females took longer developmental time, exhibited heavier body weight and longer wing length than males. Perhaps, shorter development time is more important for male mosquitoes than to achieve a bigger size as shorter developmental time helps it to win over the male-male competition for reproductive success (Bédhomme et al. 2003). Whereas for females, longer developmental time helps to achieve a bigger size which in-turn help it to have a higher reproductive success (Bédhomme et al. 2003), through increased egg production (Clements 1992). The density effects on the competitive interactions were evident in life history traits of both the mosquitoes. In comparison to the single individual treatments, larvae developing at the rear-



ing density of 2, 4 and 6, with conspecific or heterospecific individuals, showed an increased time for the age at pupation but low pupal weight, adult body weight and wing length. As shown through the DI index, the effects were more prominent for *A. aegypti* than *A. albopictus*, for age at pupation (Fig 3a), but for rest of the life history traits an opposite effect was observed (Fig 3b through 3d). The extended age at pupation resulted in bigger pupae and adults in *A. aegypti*, which would mean greater potential for longevity and fecundity, if true linear relationships are realized. Owing to the bigger size, adult *Aedes* mosquitoes, if live for longer time, increases the potential for transmission of the disease pathogen. While, laboratory (Alto et al. 2008a, b; Muturi et al. 2011a, b) and field studies (Alto et al. 2014) indicate that the smaller sized mosquitoes are more susceptible to the viral pathogens including dengue virus. Under such conditions, when the competitive interactions result in the bigger sized *A. aegypti* and smaller sized *A. albopictus*, the latter would apparently be more important in disease transmission, in compliance with the laboratory findings on viral susceptibility by *A. albopictus* (Alto et al. 2008a, b). However, field studies from Rio de Janeiro, Brazil, indicate that size-susceptibility and size-longevity analysis are not strictly linear for *A. aegypti* and females emerging from low competition conditions bear higher probability to transmit dengue virus (Juliano et al. 2014). Thus more than the disease transmission potential, the competitive advantage of *A. albopictus* is exhibited through early development with smaller size. As observed in the present instance, *A. albopictus* emerged as a smaller adult with faster development than *A. aegypti*, which may also indicate that the mosquitoes will be able to complete their life cycle faster. Considering smaller containers where the water content dwindles with time, the faster development may favour the dominance of *A. albopictus*. As a consequence, in situations where both the mosquitoes are thriving, and other conditions are congenial, *A. albopictus* may have the chance to enhance the population over *A. aegypti*, though with smaller adult size, similar to the observations made in Florida, USA (Juliano et al. 2004).

In general, the competitive outcome between *A. albopictus* and *A. aegypti* is described as context-dependent (Juliano 2009), owing to the differential outcome based on the resource availability and the environmental conditions (Moore & Fisher 1969; Daugherty et al. 2000; Yee et al. 2007; Murrell & Juliano 2008; Bara et al. 2014; Couret et al. 2014). While in many instances, the outcome is in favour of *A. albopictus* (Barrera 1996; Juliano 1998; Daugherty et al. 2000; Braks et al. 2004; Murrell & Juliano 2008), in several other situations, both species remained equal as competitors (Black et al. 1989; Ho et al. 1989; Lounibos et al. 2002; Alto et al. 2005, 2008; Murrell & Juliano 2008). Under resource based interspecific competition, *A. albopictus* outcompetes *A. aegypti* in instances when the food resources are of plant origin and the temperature conditions range between 20°C and 35°C

(Farjana et al. 2012). However, availability of the animal food resources (Daugherty et al. 2000) shifts the competitive advantage in favour of *A. aegypti*. In the present instance, the density dependent competitive interactions was observed, where effects of interspecific competition was significant for *A. aegypti* alone. A deviation in this observation may occur depending on the quality and quantity of resources available in the natural habitats. However, the outcome of competition on the life history traits at high density levels (Alto et al. 2008a) was also realized in the present instance with low density, possibly indicating the invariant property of density effects on life history traits and thus the effective vectorial capacity. Further studies including density, resource quality and habitat permanence as explanatory variables should be carried out to define the competition outcome involving *A. aegypti* and *A. albopictus*, with higher precision.

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