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ORIGINAL RESEARCH ARTICLE

Effect of ABO and Rh blood groups on host preference, oviposition success, and development of laboratory-reared *Aedes aegypti*

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Abstract

Aedes aegypti is the primary dengue vector in Sri Lanka that causes the massive public health problem of Dengue Fever (DF) and Dengue Hemorrhagic Fever (DHF) on the island. It is an anthropophilic mosquito that shows preferential feeding depending on the host blood type. Hence, the study was conducted to investigate the effects of human ABO and Rh blood groups on host attractiveness, feeding, oviposition and other life-history traits of *Aedes aegypti*. Data of DF and DHF patients were collected from some selected hospitals in the Western province. Subsequently, mated female *Ae. aegypti* mosquitoes were exposed to eight blood groups (A^-, A^+, B^-, B^+, AB^-, AB^+, O^-, O^+) using human volunteers to investigate the landing and feeding preferences. Furthermore, oviposition success, adult longevity, progeny longevity, larval duration, larval mortality, pupal duration, and adult fecundity were examined. Accordingly, people with the O^+ blood group were the most typical group infected with DF and DHF in 2017 and 2018. However, the peak landing and feeding preferences were observed for O^-. Besides, the current findings indicated that human ABO and Rh blood types did not significantly affect life-history parameters including oviposition success, larval duration, pupal duration, larval mortality, adult longevity, progeny longevity, and fecundity of *Ae. aegypti.* Eventually, it can be concluded that dengue infection risk varies with the ABO and Rh blood groups depending on their unequal prevalence in the community as well as their association with mosquito performance.

Keywords *Aedes aegypti* · Blood groups · Feeding · Landing · Life-history

Introduction

Currently, Dengue Fever (DF) and Dengue hemorrhagic Fever (DHF) have become critical health problems in Sri Lanka. It is a viral infection caused by four different serotypes, namely DENV-1, DENV-2, DENV-3, and DENV-4 (Sirisena and Noordeen 2016). The two major mosquito vectors transmitting the dengue viruses in Sri Lanka are *Aedes aegypti* and *Aedes albopictus* (Noordeen et al. 2018) where *Ae. aegypti* is the primary vector and *Ae. albopictus* is the secondary vector (Vitarana et al. 1997; Crawford et al. 2017).

Plant sap serves as the energy source, whereas vertebrate blood is the amino acid source that helps the performance of mosquitoes (Greenberg 1951; Foster 1995). Generally, mosquitoes have a preferential selection of host species for blood meals (Tandon and Ray 2000). The host preference is affected by various intrinsic and extrinsic factors. Genetic selection being the basis of these inherent factors, is controlled by adaptive advantages, which result in feeding on a specific host species (Kaipainen and Vuorinen 1960). In addition to the genetic basis of the host preference, the density of host species and accessibility to the blood source also affect the host preference. The host selection behaviour correlates with most vectors of vector-borne diseases (Takken and Verhulst 2013).

The odours released by human skin vary from person to person depending on the blood type, and mosquitoes can perceive these slight variations (Qui et al. 2006). Consequently, the variation in odours plays a significant role in the anthropophilic nature of mosquitoes. Several studies have shown that mosquitoes prefer certain blood groups over others. Accordingly, *Anopheles gambiae* feeds preferentially on blood group O under laboratory conditions (Wood and Harrison 1972). The basis for this preference is unknown. It may be related to the availability of ABO substances on skin cells and secretions in sweat (Gupta and Chowdhuri 1980). Furthermore, Gupta and Chowdhuri (1980) stated

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that different blood groups have different susceptibilities to malarial infection.

Female mosquitoes require both sugar and blood meal to gain their full reproductive performance (Foster 1995; Morrison et al. 1999). Blood is used for both energetic and reproductive requirements, benefitted from its anthropophilic nature (Takken and Verhulst 2013). Proteins are an essential requirement for egg production in mosquitoes (Gonzales and Hansen 2016; Pitt 2014). The protein concentration in a host blood meal determines the degree of oogenesis. Micronutrients in the blood such as iron, cholesterol, and amino acids facilitate mosquito reproductive performance. The iron bound to heme in hemoglobin accumulates in the ovaries and eggs of the mosquito. Furthermore, certain amino acids are required for vitellogenesis (Gonzales and Hansen 2016).

Antigens on the red blood cells (RBC) cell surface determine human blood groups. In the human population, there are two main blood group classifications as ABO (blood types A, B, AB, and O) and Rh (Rh D-positive or Rh D-negative blood types) (Dean 2005). The ABO blood grouping distinguishes the presence or absence of two carbohydrate antigens (A and B) on the RBC membrane and three specific antibodies (Anti-A, anti-B, anti-A, B) present in the blood plasma (Mattos 2016).

Subsequently, it was hypothesized that human ABO and Rh blood groups show an association with DF and DHF. Thus, the objective of the present study was to investigate the effects of human ABO and Rh blood groups on host attractiveness, feeding, oviposition and other life-history traits of *Aedes aegypti*.

Materials and methods

Study area and test insects

Aedes aegypti eggs were brought from the Molecular Medicine Unit, Faculty of Medicine, University of Kelaniya. A pure colony was maintained during the entire study period in the insectary at the University of Kelaniya (6°58′20.91" N; 79°54′52.83" E) under a temperature of $27 \pm 2\ ^{0}$C, relative humidity 75–80%, and photoperiod of 12L: 12D.

Maintaining the mosquito colony

An egg sheet of *Ae. aegypti* was placed in a 750 mL plastic tray (15.0 cm × 10.0 cm × 5.0 cm) where two-thirds of it was filled with water first boiled up to 100 °C and cooled to room temperature (Zheng et al. 2015). After 24 h, the hatched first instar larvae (L1) were counted and transferred to another 750 mL plastic trays, with 100 larvae per tray. Laval trays were covered with a net with having 0.5 mm mesh size to prevent oviposition by other mosquito strains or insects. The larvae were fed with a liquid diet prepared by the finely ground krill (*Euphausiacea sp.*). First, second, third, and fourth instar larvae were supplied with 5 mL, 6 mL, 7 mL, and 8 mL of the liquid diet respectively, twice daily until pupation. Water was carefully siphoned out from the trays daily and replaced with new aerated tap water to maintain the water quality of the larval rearing medium. Subsequently, the pupae were collected using a plastic pipette and reassigned to a 500 mL beaker containing aerated tap water. The beaker was kept inside a mosquito rearing cage until the emergence of adults. The cage was made of a wooden frame (30 cm × 30 cm × 30 cm) with all sides covered with a mosquito-proof mesh. A 50 cm sleeve opening was built in the front panel for the maintenance purposes of the colony (Fig. 1). The newly emerged adults were fed with a 10% sugar solution continuously for two days (Helinski and Harrington 2011; Zheng et al. 2015). Mating was eased within the same cage since the males and females were together, and it was confirmed by visual observation when mating copulas had been formed. Consequently, the blood-feeding was followed by a 24-h starvation period.

Distribution of ABO and Rh blood groups among non-infected people, dengue fever (DF) and dengue hemorrhagic fever (DHF) patients in the Western province

Data related to the distribution of ABO and Rh blood groups among the people in the Western province, Sri Lanka were obtained from the National Blood Transfusion Service, Narahenpita.

Similarly, to determine the distribution of ABO and Rh blood groups among DF and DHF patients, demographic data concerning human blood groups were collected from hospital admissions for 2017 and 2018. Five government general and base hospitals in the Western province of Sri Lanka were randomly selected for this purpose (i.e., Base hospital Panadura, Base hospital Horana, Base hospital Kiribathgoda, General hospital Kalutara, Lady Ridgeway hospital).

Effect of ABO and Rh blood groups on landing preference, feeding preference, oviposition success, life-history parameters, longevity, and fecundity of *Aedes aegypti*

Experiments were carried out to assess the effect of ABO and Rh blood groups on (i) landing preference, (ii) feeding preference, (iii) oviposition success, (iv) life-history parameters (v) longevity, and (vi) fecundity of female *Ae. aegypti*. For these experiments, four days old mated female mosquitoes were used and they were exposed to eight blood groups (A^-, A^+, B^-, B^+, AB^-, AB^+, O^-, O^+) for 20 min.

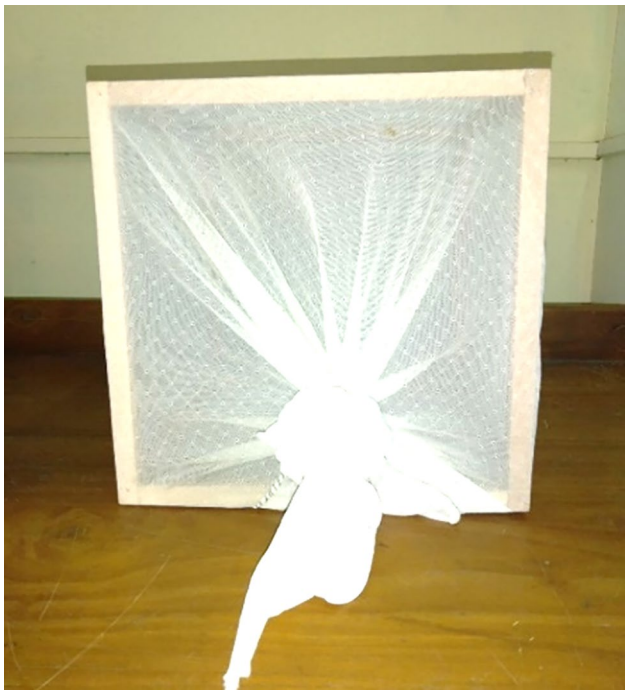

Fig. 1 Mosquito rearing cage (30 cm × 30 cm × 30 cm)

(i) Landing preference

A cage made up of a wooden frame (100 cm × 60 cm × 30 cm) with all sides covered with a mosquito-proof mesh was used. Eight sleeve openings (50 cm) were located around four sides of the cage (Fig. 2). Hundred mated females were released into the cage. Subsequently, the human volunteers with different blood groups (A^-, A^+, B^-, B^+, AB^-, AB^+, O^-, O^+) presented one hand through the eight individual openings. The hand was held still for 20 min. The number of mosquitoes that alight on the hands of eight volunteers was recorded separately every 30 s for 15 min.

(ii) Feeding preference

The female mosquitoes that were used to assess the effect of landing preference were used here. After 20 min of exposure to eight human volunteers, females were euthanized using ethyl acetate. Subsequently, the number of mosquitoes who have fed on different blood groups was determined with direct agglutination tests using anti-A, anti-B, and anti-Rh.

(iii) Oviposition success

Four days old, starved 20 female mosquitoes were allowed to feed on one selected blood group within a rearing cage. The procedure was repeated for all the eight types of blood groups A^-, A^+, B^-, B^+, AB^-, AB^+, O^- and O^+. Afterwards, ten fully engorged females fed on each blood group were transferred into another mosquito rearing cage and an oviposition trap was placed in each cage. Black colour cylindrical plastic cups (200 mL) with a diameter of 7.0 cm and a depth of 6.0 cm were used to prepare the oviposition substrates. The cups were soaked in a water bath for one week to avoid the lousy plastic odour. A filter paper stripe of length 22.0 cm and width of 5.0 cm was placed along the plastic cup's interior circumference, which acted as the substrate for egg-laying. One-third of the cup was filled with

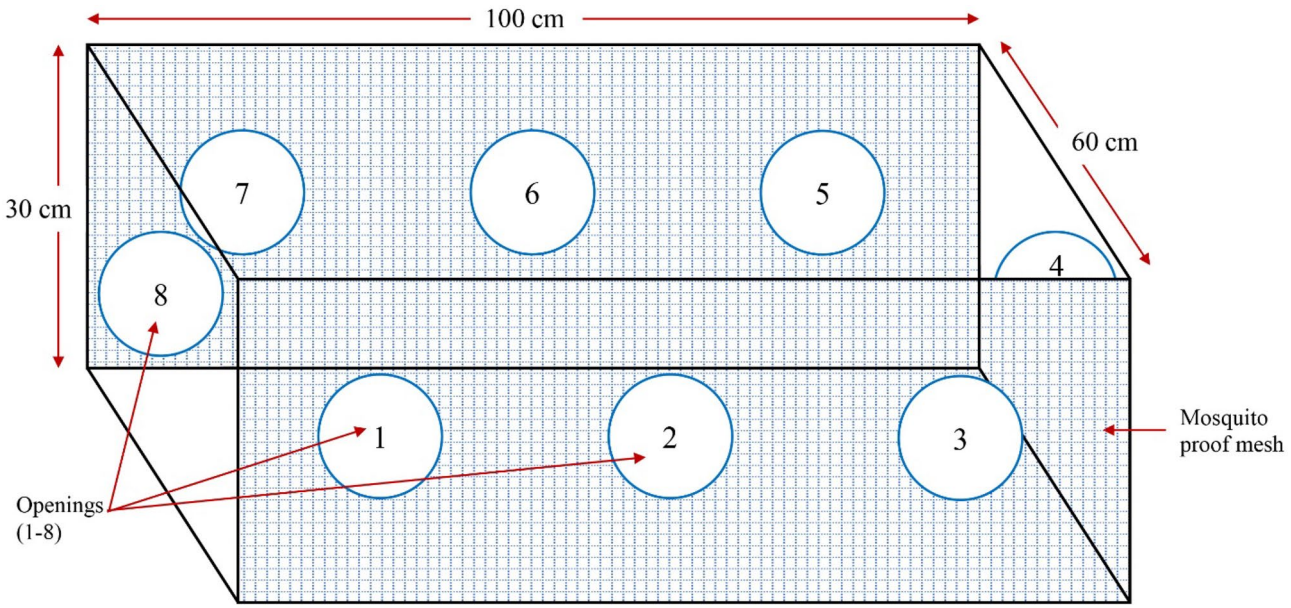

Fig. 2 Cage used to present the arms of the eight volunteers to assess the landing preference of *Aedes aegypti*

aged tap water. The number of eggs laid was counted using a low-power stereo microscope at 15X magnification after 132 h of exposure to the blood meal.

(iv) Life-history parameters

After oviposition, the egg sheet was placed on a 2 L tray filled with water boiled up to 100 °C and cooled to room temperature. Twenty-four hours later, 50 first instar larvae were counted from each blood group and transferred separately to another 2 L plastic trays. Larval mortality, total larval duration, and pupal duration were recorded.

(v) Fecundity

Ten female mosquitoes from each blood group that emerged from the (iv) life-history parameters experiment were killed with ethyl acetate. The right wing of each adult was removed at the time of dissection and mounted on a glass microscope slide in a small drop of distilled water. The wing length was measured from the axial incision to the apical end of the wing using a compound microscope (Olympus© CX21) (Schneider et al. 2004). The wing was aligned along an ocular micrometer (1 ocular unit, 0.025 mm at 40X) (Menge et al. 2005).

(vi) Longevity

Twenty female mosquitoes fed with each blood type were transferred to separate mosquito rearing cages. Similarly, twenty female mosquitoes that emerged from each blood group of the (iv) life-history parameters experiment were fed with the same blood type used for the parents and transferred to mosquito rearing cages. Each day, the number of dead females was recorded until the adult population size became zero to determine the adult and progeny longevity. The days required for the adult population to become zero were considered longevity. The mosquitoes were regularly provided with their relevant blood meal.

All the experiments were repeated three times under the same laboratory conditions to improve the accuracy of the results.

Statistical analysis

Data obtained during the experiments were analyzed using Minitab 14 software. All the data were subjected to the Anderson–Darling normality test. Since the data followed a normal distribution, a one-way analysis of variance (ANOVA) was carried out to check whether ABO and Rh blood groups significantly affected landing preference, feeding preference, oviposition success, life-history parameters, longevity and fecundity of *Aedes aegypti*. Furthermore, one-way ANOVA was used to determine whether there is a significant difference in the ABO and Rh blood groups among non-infected people, dengue fever (DF) and dengue hemorrhagic fever (DHF) patients in the Western province. Tukey's test was used to test the differences among sample means for significance.

Results

Distribution and association of ABO and Rh blood groups with dengue infection status in the Western province, Sri Lanka

Human ABO blood group distribution in the Western province has shown a significant difference (ANOVA, $F_{7, 16} = 311.48$, $P < 0.05$). Accordingly, O^+ was the most abundant blood group among the people. It was followed by B^+, A^+ and AB^+ respectively. Subsequently, they were trailed by the Rh-negative types O^-, B^-, A^- and AB^- (Fig. 3).

The relationship between dengue infections and different human blood groups was evaluated. In 2017, there was a significant association between dengue fever and different blood groups (ANOVA, $F_{7, 24} = 3.09$, $P < 0.05$). The highest number of DF patients were recorded for the blood group O^+ followed by B^+, A^+, and AB^+ respectively. The least number of DF patients were recorded from the blood groups AB^-, A^-, B^-, and O^- respectively. The same pattern was observed for the DHF patients in 2017 (ANOVA, $F_{7, 24} = 11.85$, $P = 0.05$; Fig. 4).

Similarly, the DF patients showed a significant variation with blood groups in 2018 (ANOVA, $F_{7, 24} = 5.07$, $P < 0.05$). The highest number of DF patients were recorded for the blood groups of O^+ followed by B^+, A^+, and AB^+ respectively. The least number of DF patients were recorded from the blood groups of AB^-, A^-, B^-, and O^- respectively. The same pattern was observed for the DHF patients in 2018 (ANOVA, $F_{7, 24} = 3.24$, $P < 0.05$; Fig. 4).

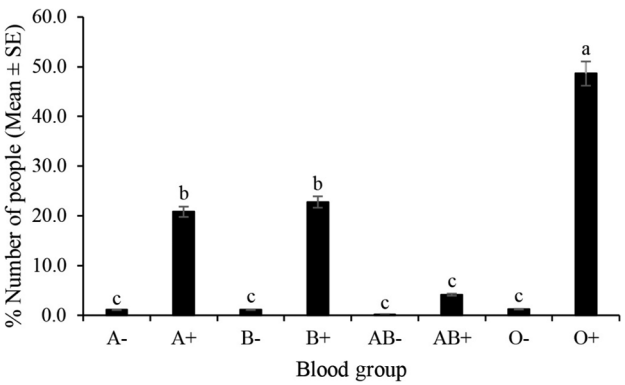

Fig. 3 Distribution of ABO and Rh blood groups among the people in the Western province. Error bars represent the SE of the mean

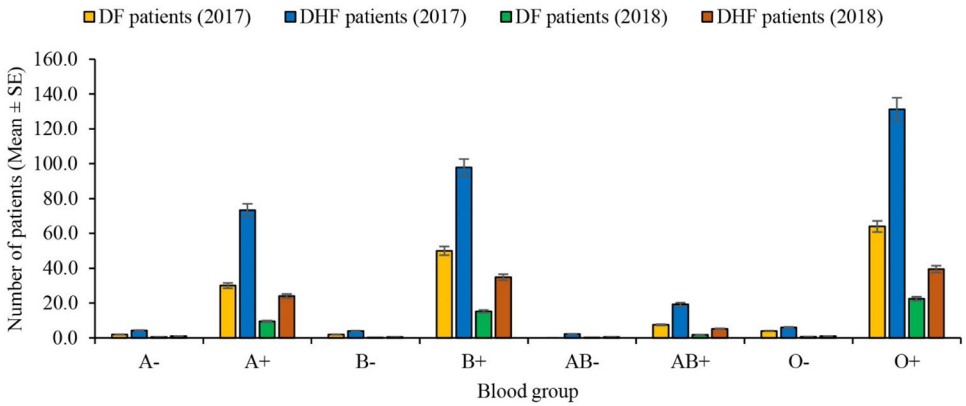

Fig. 4 Distribution of ABO and Rh blood groups among DF and DHF patients in 2017 and 2018. Error bars represent the SE of the mean

Landing preference, feeding preference, oviposition success, life-history parameters, longevity, and fecundity of *Aedes aegypti* with ABO and Rh blood groups

When mated females were allowed to land on the hands of eight volunteers having different types of blood, it was observed that there was a significant attraction towards some blood groups (ANOVA, $F_{7, 16} = 1.12$, $P < 0.05$). Accordingly, *Ae. aegypti* landed more frequently in O^- blood group followed by O^+, A^- and A^+ blood groups. The least number of mosquitoes had been attracted to B^+ followed by B^-, AB^+ and AB^- blood groups (Fig. 5).

Moreover, the results showed a significant difference in the feeding preference of *Ae. aegypti* on different blood groups (ANOVA, $F_{7, 16} = 3.36$, $P < 0.05$). The highest preference was observed for the O^- blood group followed by O^+, A^-, A^+, and AB^+. Comparatively, a less feeding preference was shown for the blood groups AB^-, B^+, and B^- (Fig. 6a).

However, there was no significant influence of blood groups on the oviposition success of *Ae. aegypti* mosquitoes (ANOVA, $F_{7, 40} = 1.26$, $P > 0.05$; Fig. 6b). Similarly, the life-history parameters including larval mortality (ANOVA, $F_{7, 24} = 0.25$, $P > 0.05$; Fig. 6c), total larval duration (ANOVA, $F_{7, 16} = 0.00$, $P > 0.05$; Fig. 6d) and pupal duration (ANOVA, $F_{7, 24} = 1.00$, $P > 0.05$; Fig. 6e) did not show any significant difference with the ABO and Rh blood groups.

Furthermore, the fecundity of the newly emerged females who had been nourished with different blood groups did not show any significant variation with the ABO and Rh blood groups (ANOVA, $F_{7, 16} = 0.60$, $P > 0.05$; Fig. 6f).

Correspondingly, adult longevity (ANOVA, $F_{7, 16} = 0.77$, $P > 0.05$; Fig. 7a) and progeny longevity (ANOVA, $F_{7, 16} = 0.52$, $P > 0.05$; Fig. 7b) of female *Ae. aegypti* were not significantly affected by different ABO and Rh blood groups. Parent adult population and newly emerged adults (progeny) survived around 18–20 days despite the type of blood-fed.

Discussion

The primary dengue vector *Ae. aegypti* is a highly anthropophilic mosquito that frequently feeds on human blood over the other vertebrate blood such as bovine and avian (Tandon and Ray 2000). Limited studies have been conducted in Sri Lanka to assess the relationship between dengue fever and the human ABO and Rh blood groups. However, the main objective of the present study was to obtain the association between reproductive and developmental performances of *Ae. aegypti* mosquitoes with human ABO and Rh blood groups. As supplementary supportive information, the demographic data on blood groups of dengue-infected patients in 2017 and 2018 were obtained from some selected hospitals in the Western province of Sri Lanka.

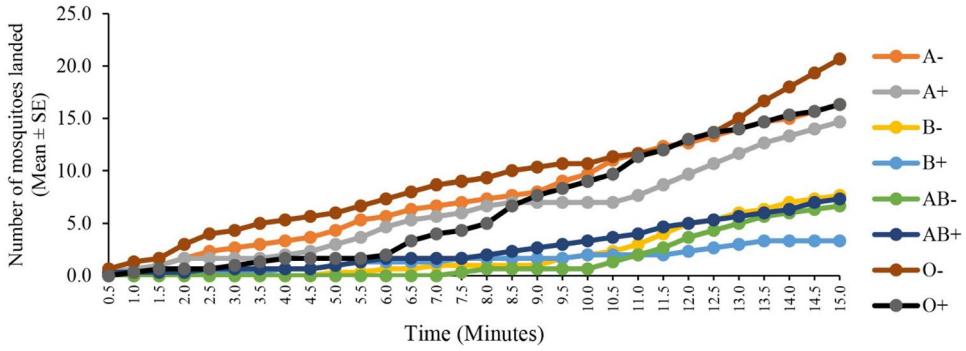

Fig. 5 The number of *Aedes aegypti* mosquitoes landed on different human ABO and Rh blood groups with time

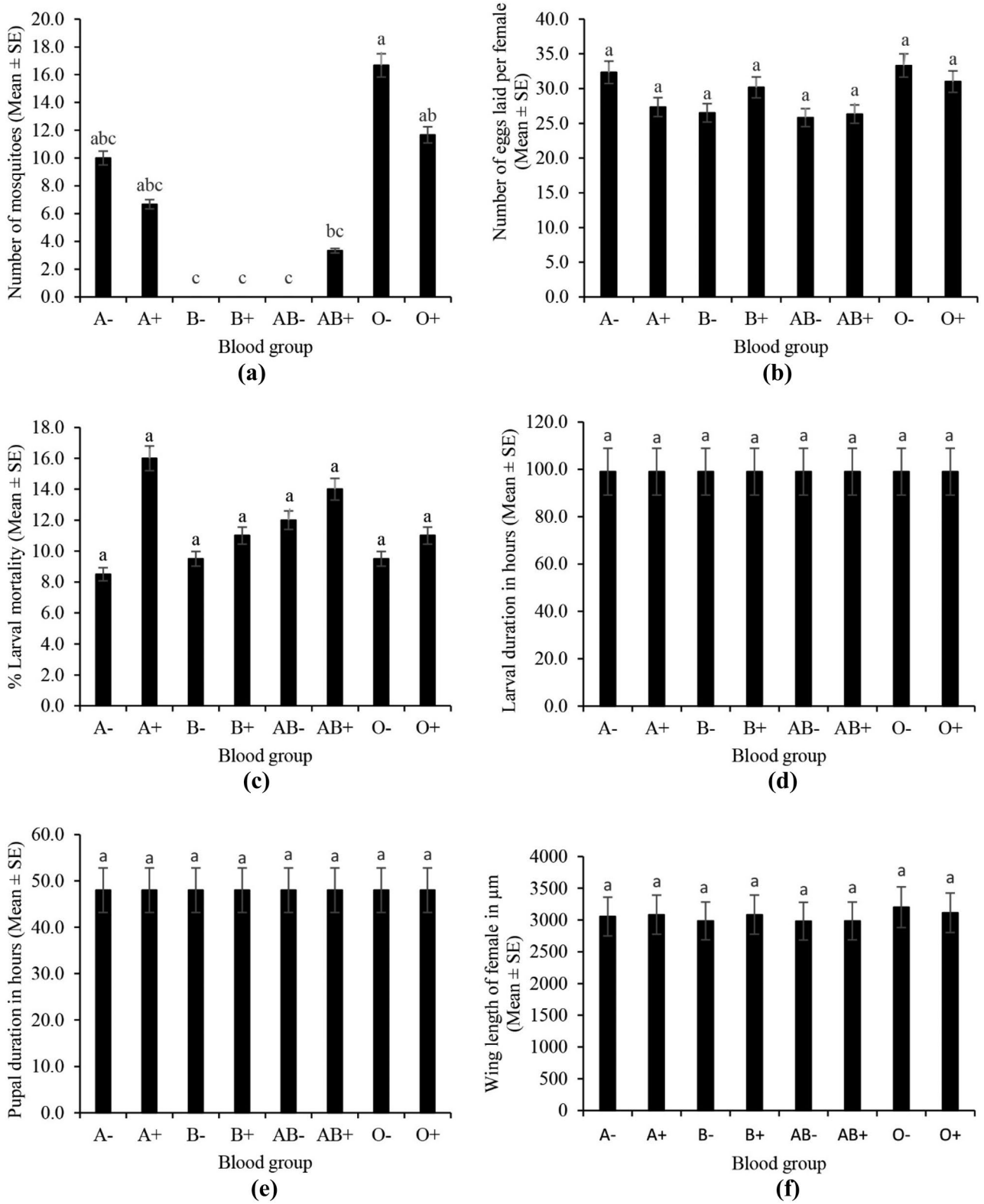

Fig. 6 **a** Feeding preference **b** oviposition success **c** percentage larval mortality **d** total larval duration **e** pupal duration **f** fecundity of female *Aedes aegypti* with different human ABO and Rh blood groups. Error bars represent the SE of the mean

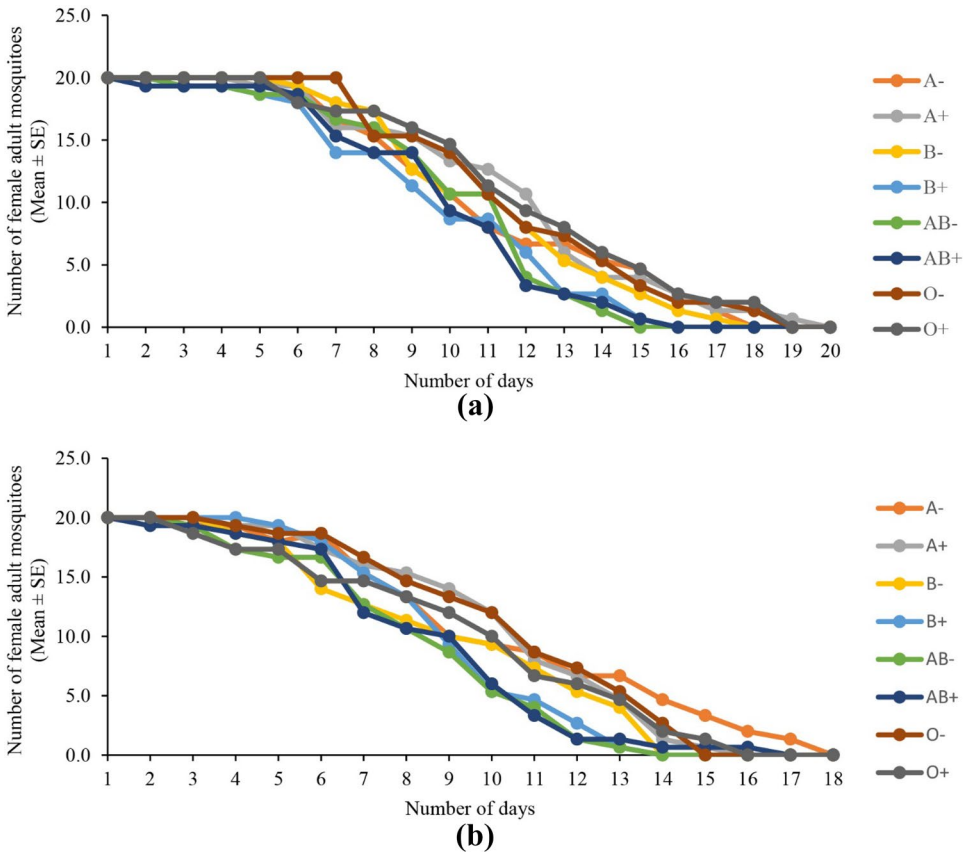

Fig. 7 **a** Adult longevity **b** progeny longevity of female *Aedes aegypti* with ABO and Rh blood groups

Accordingly, the present study investigated the preference of *Ae. aegypti* for the eight major human blood groups and analyzed whether the blood group preference affected the mosquito performances in reproduction and development. The results indicated that different ABO and Rh blood groups caused a significant variation in the landing and feeding preferences in the laboratory-reared *Ae. aegypti* mosquitoes. However, oviposition success, fecundity, longevity and life history parameters were not affected.

Investigations have unveiled that infection of dengue is not confined to one factor. Instead, the serotype of the infecting virus, the patient's age, and the patient's genetic background can be accounted for both DF and DHF. Also, research has discovered that predisposition to dengue disease can be determined by human leukocyte antigen (HLA) haplotype (Weiskopf et al. 2013; An et al. 2004). The HLA present on the cell surface functions as an antigen-presenting molecule and the polymorphism of HLA can change an individual's immune response (Lan et al. 2008). Since the ABO blood group system is a part of the innate immune system, it has been shown that individuals with different ABO blood groups differ in their susceptibility or resistance to viral and bacterial infections and diseases. Meanwhile, Kaipainen and Vuorinen (1960) hypothesized a relationship between blood group, gene, and disease. Supporting the previous research studies, the current study determined that the dengue infection status is correlated with the ABO and Rh blood group distribution in Sri Lanka. Accordingly, most DF and DHF patients in the Western province were O^+ followed by B^+, A^+, and AB^+ blood groups. A similar association of human ABO blood groups with DF and DHF has been witnessed in a study that utilized the demographic data of dengue patients collected from hospitals (Khode et al. 2013). Moreover, the abundance of the blood groups among non-infected people in the Western province followed a similar occurrence to the distribution of blood groups among DF and DHF patients. Furthermore, some studies have discovered that the most common blood group in Sri Lanka is O^+ followed by B^+, A^+, AB^+ and the hostile blood groups are of most minor abundance (Bulugahapitiya and Satarasinghe 2011). Hence, there is an increased risk of people having an O^+ blood group infected with dengue or dengue hemorrhagic fever.

The experiments carried out using human volunteers showed the landing and feeding preferences of *Ae. aegypti* were significantly different among the ABO blood groups. This may be due to the factors like thermal variation and the quality of the blood source. The thermal cues may be higher than the chemical cues exerted by the blood source. Furthermore, these variations may occur due to odour released by the skin, skin emanation, skin colour, and other factors

like metabolic rate and stimulatory components in blood that cause an attraction of mosquitoes. The differences in odour production may be quantitative, qualitative, or both (Qui et al. 2006). Nevertheless, it did not allow mosquitoes to reject any blood group. Thus, in the current study, mosquitoes landed and fed more frequently in the O^- blood group followed by O^+, A^-, and A^+. It may be because the stimulatory response of blood type O has a strong attraction for *Ae. aegypti* mosquitoes over the other groups. Researchers have shown that the preference of *Ae. albopictus* and *Ae. aegypti* is more towards the blood group O than blood group A and B (Shirai et al. 2004; Wood 1976). Although the most preferred blood group of *Ae. aegypti* was O^-, the highest number of DF and DHF-infected patients had the O^+ blood group. That is because the usual prevalence of the O^+ blood group is higher in the community than O^- blood group.

Humans' secretor and non-secretor status is another factor responsible for mosquitoes' attraction. Some people emit oligosaccharide substances and soluble A, B, and H antigens of blood on the skin. These substances are responsible for the variation of host preference in mosquitoes. Shirai et al. (2004) stated *Ae. aegypti* has a preferential selection on blood group O secretors than its non-secretors and group A non-secretors than its secretors. However, Shirai et al. (2004) explain the attraction of *Ae. aegypti* preferably for the type O blood group as mosquito evolution happened in Africa where the O blood group was more abundant. Finally, it was revealed that, *Ae. aegypti* had the highest frequency of biting on the most abundant blood groups (Rh^+) in the population and the least frequency of biting on the least abundant blood groups (Rh^-).

Several components in the human blood can influence egg production in mosquitoes. It has been reported that the low level of isoleucine found in human blood is the limiting factor for egg production when *Ae. aegypti* feeds on humans (Harrington et al. 2001; Gonzales et al. 2015; Greenberg 1951). However, the isoleucine concentrations of different human blood groups were not investigated in the present study. Consequently, the oviposition success was determined by the number of eggs laid during the first gonotrophic cycle. Thus, only one gonotrophic cycle was considered in this study to avoid overlapping of gonotrophic cycles. Since most of the female mosquitoes died after the first gonotrophic cycle, the accuracy would have been lowered if they were pushed to the second gonotrophic cycle. The results discovered no significant variation in the number of eggs laid with different blood groups. This may be due to the lack of variation in nutrient composition in different blood types, which facilitate a nutrient reserve during the larval and pupal developmental periods. Moreover, high amounts of yolk protein can contribute to more eggs. Hence, the current results indicate that variation in serum protein amounts and other nutritional elements in different blood groups are not different. They give rise to the same number of eggs.

The life history parameters such as larval duration, pupal duration and larval mortality were observed during the experiment. The larval food was served as the only nutrient source for the entire larval period. However, the results indicated no significant effect on any of the life history parameters. Furthermore, the longevity of the adult female mosquitoes was determined while providing a blood meal every day until the last female died. Nayar and Sauerman (1975) stated that blood meal provides sufficient reserves to enable the mosquito species to survive long enough to produce eggs. It was observed that there was no significant effect on the longevity of parent mosquitoes with specific blood groups. Correspondingly, the laid eggs were allowed to hatch, and the same procedure was repeated to find the progeny longevity. Still, the results showed no effect on progeny longevity.

The fecundity of female mosquitoes was obtained by measuring the right-wing length. According to the present study, it was observed and confirmed that the eight different blood groups did not influence the fecundity. Thus, the fitness of the mosquitoes is not affected by the nutrient content in each blood type. The same larval diet was provided with proper amounts, and the environmental parameters were kept almost unchanged during the experimental period. Therefore, any variation in body size could be correlated with the nutrient amount of the blood group. A study conducted irrespective of the Rh factor revealed that though there is a significant difference in feeding preference, there is no difference in the fecundity of female mosquitoes in the new progeny (Prasadini et al. 2019).

The yolk is the food source of the developing embryo once the fertilized eggs are laid. A balanced mixture of amino acids in the blood meal facilitates yolk synthesis. Yet there is a small nutrient value of egg yolk for gravid females (Telang 2006). Since there was no difference in the life history parameters, longevity, and fecundity relevant to eight blood groups, it can be assumed that the nutrients, specifically the amino acids present in different blood groups, are the same. As Olayemi et al. (2011) report, it is possible that the female mosquito consumed the entire blood meal for egg development and maturation. However, further studies are required to obtain a better insight into the effects of the nutrients in different blood groups on the performances of *Ae. aegypti* mosquitoes.

From the time when the findings discovered that the most preferred blood group of *Ae. aegypti* is O^- followed by O^+, and the knowledge is applicable to identify the areas with a high risk of DF and DHF infection by looking into the existence of blood groups in the area.

Author contribution GASMG designed the study. GKDNG wrote the manuscript. GKDNG and RAKMG contributed to the data analysis. GASMG, RAKMG and DPWJ reviewed the manuscript. RAKMG and DPWJ edited the manuscript. All authors have read and agreed to the final version of this manuscript.

Declarations

Conflict of interest statement The authors declare that they have no competing interests.

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