Is the body size of *Aedes aegypti* (Diptera: Culicidae) a determinant in the epidemiological dynamics of dengue?: a perspective to be considered within vector control programs

¿Es el tamaño corporal de *Aedes aegypti* (Diptera: Culicidae) un determinante en la dinámica epidemiológica del dengue?: una perspectiva a considerar dentro de los programas de control de vectores

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¿Es el tamaño corporal de *Aedes aegypti* (Diptera: Culicidae) un determinante en la dinámica epidemiológica del dengue?: una perspectiva a considerar dentro de los programas de control de vectores

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ABSTRACT

It has been proposed that the high incidence of dengue is related to the increase in vector population density although this fact does not apply to all endemic areas. The body size of the adult mosquito is modulated by habitat conditions in immature stages and could affect epidemiological dynamics of dengue, since it has been suggested that size affects vectorial capacity, at least in laboratory conditions; field studies are scarce, and there is no scientific consensus on the relationship between body size and epidemiology of the disease. In this context, there is a possibility that a body size highly competent in dengue virus transmission may emerge in epidemic periods. For this reason, the study of the temporal fluctuation of the vector would help determine the viral size-transmission relationship, and integrated control methods could be implemented on this basis to establish body sizes with a low probability of transmission, mainly during periods of high epidemiological incidence. Factors related to the behavior and life history of *Aedes aegypti* are discussed, as well as the importance of temporal monitoring of adult mosquito body size in endemic areas.

Key words: *Aedes aegypti*, vector capability, epidemiological dynamics-dengue, vector control.

RESUMEN

Se ha propuesto que la alta incidencia de dengue está relacionada con el aumento en la densidad de la población del vector, aunque este hecho no se aplica a todas las áreas endémicas. El tamaño corporal del mosquito adulto está modulado por las condiciones del hábitat en las etapas inmaduras y podría afectar la dinámica epidemiológica del dengue, ya que se ha sugerido que el tamaño influye en la capacidad vectorial, al menos en condiciones de laboratorio; los estudios de campo son escasos y no hay consenso científico sobre la relación entre el tamaño corporal y la epidemiología de la enfermedad. En este contexto, existe la posibilidad de que durante los períodos epidémicos surja un tamaño corporal altamente competente en la transmisión del virus del dengue. Por esta razón, el estudio de la fluctuación temporal del vector ayudaría a determinar la relación entre el tamaño y la transmisión, y se podrían implementar métodos de control integrados con base en esto para establecer tamaños corporales con baja probabilidad de transmisión, principalmente durante períodos de alta incidencia epidemiológica. Se discuten factores relacionados con el comportamiento y la historia de vida de Aedes aegypti, así como la importancia del monitoreo temporal del tamaño corporal del mosquito adulto en áreas endémicas.

Keywords: *Aedes aegypti*, capacidad vectorial, dinámica epidemiológica, dengue, control vectorial.

Introducción

Dengue is a public health concern in tropical and subtropical regions of the world which is estimated to affect about 390 million people each year (Bhatt et al., 2013). The etiologic agent is dengue virus (DENV), a flavivirus belonging to the Flaviviridae family transmitted to humans mainly by hematophagous females of *Aedes aegypti* Linnaeus, 1762. Since DENV transmission is mediated by mosquitoes, changes in vector populations will necessarily be reflected in the epidemiological dynamics of the disease (Morin et al., 2013).

In dengue endemic regions, the incidence of the disease has a consistent annual pattern with clearly marked temporal increases that could be explained by the increase in mosquito density (Morin et al., 2013). However, an increase in mosquito population is not a determinant of infection risk in all regions where dengue is a public health issue (Estallo et al., 2020). In this context, it has been generalized that vector abundance is positively correlated with the amount of rainfall (Morin et al., 2013); regardless, this relationship does not explain the epidemiological configuration in different endemic areas such as Hong Kong (Yuan et al., 2020).

Some authors have cataloged the interaction between environment and dengue cases as complex (Sharmin et al., 2015; Zhu et al., 2016).

From a morphometric point of view, it has been contemplated that the body size of the adult mosquito could modulate the transmission of DENV, mediated by environmental (e.g., temperature and humidity) and competitive (intraspecific or interspecific) factors from larval habitats (Sumanochitrapon et al., 1998; Alto et al., 2008; Kanget al., 2017; Jeffrey-Gutiérrez et al., 2020), which could vary in time and space.

According to the competition-longevity hypothesis, greater competition among larvae reduces the size of adults, and larger longer-lived *Ae. aegypti* females from low competition environments have increased probability of disseminated infection and viral transmission (Juliano et al., 2014). In contrast, the competition-susceptibility hypothesis indicates that physiological processes are more important than longevity, and competition among larvae results in smaller adults, and smaller adults are more susceptible to dengue infection (i.e., have greater vector competence) (Alto et al., 2008; Juliano et al., 2014).

It is important to implement vector surveillance measures focused on the body size of the adult mosquito to determine its relationship with the epidemiological dynamics of dengue and the highly competent thresholds of susceptibility and viral transmission and, based on this, mitigate control measures aimed at establishing sizes of *Ae. aegypti* with low or no risk of transmission of the etiologic agent.

Larval competition and its relation to adult emergence

Larval competition is mediated by one species (intraspecific) or by different species (interspecific) living in the same habitat. These interactions are dependent on immature density and nutrient availability and describe the development and growth up to the adult stage (Clements, 1992). Pupation usually takes place under a minimum size mediated by nutrient reserves in the larval stage, reserves which are a biological indicator of nutritional conditions (Clements, 2000).

The mass and body size of the adult are largely determined by the mass of the pupae, which, in turn, are dependent on the ability to acquire and conserve nutrients in the larval stage (Clark et al., 2004). Therefore, factors that cause energy expenditure or reduce nutrient assimilation in larval hatcheries will necessarily be reflected in the biological indicators mentioned above (Clark et al., 2004) (Fig. 1A, B, C). The results of competition in *Ae. aegypti* are well established and greater competition generally has a positive correlation with developmental time and a negative association with larval survival and pupal and adult body size (Braks et al., 2004; Alto et al., 2015). Other measures such as

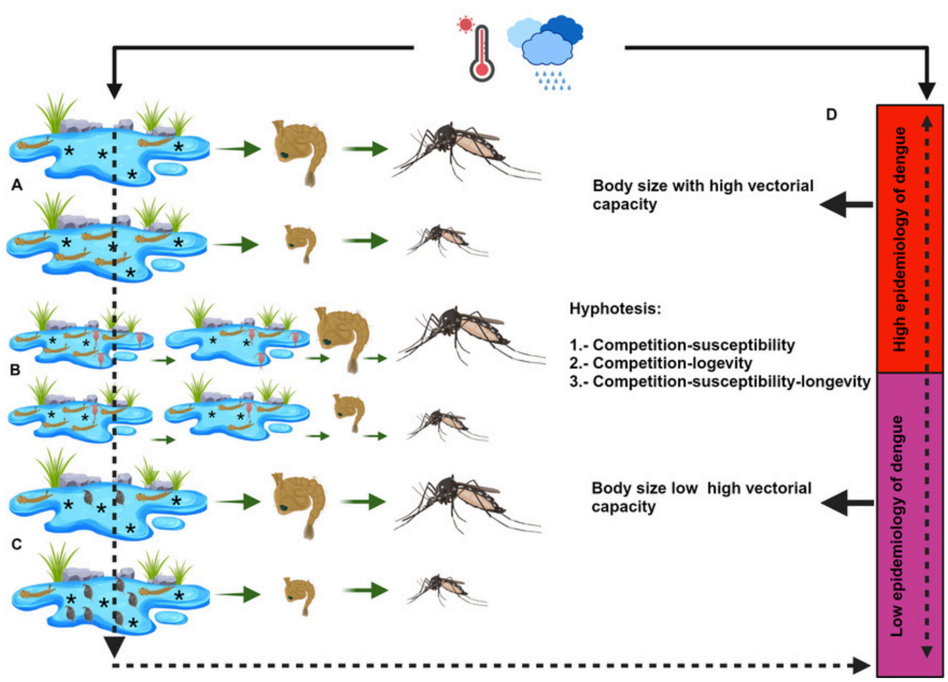

Figure 1. Diagram that indicates the relationship between larval habitats and the development and growth towards the adult of *Aedes aegypti*, as well as its possible relationship with the epidemiological dynamics of dengue in periods of low and high incidence of the disease. A, Intraspecific competetition. B, Depredation. C, Interspecific competition. D. Epidemiological fluctuation of dengue.

larval body length and pupal cephalothorax length have been proposed as efficient indicators of nutritional competition (Gunathilaka et al., 2019).

It has been observed that larval competition has a relationship with sex ratio and adult emergence time of *Ae. aegypti*. Different studies indicate that under interspecific competition males develop faster than females (Chandrasegaran et al., 2018). In mosquitoes, females, are larger in their adult stage than males, and have longer emergence times (Chandrasegaran et al., 2018). Likewise, as they spend more time interacting in their habitats, they are exposed to environmental conditions for a longer period of time, causing a higher larval mortality rate compared to males; however, the amount of nutrients available in the natural environment could compensate for the development and emergence time of females, thus balancing the sex ratio in the environment (Gunathilaka et al., 2019).

It has been reported that increased intraspecific competition of *Ae. aegypti* and interspecific competition with Ae. *albopictus* Skuse 1895 and *Culex quinquefasciatus* Say, 1823 increase traits such intraspecific competitions; however, contradictory results have been observed regarding the competitive dominance of the species (Alto y Bettinardi, 2015). These differences could

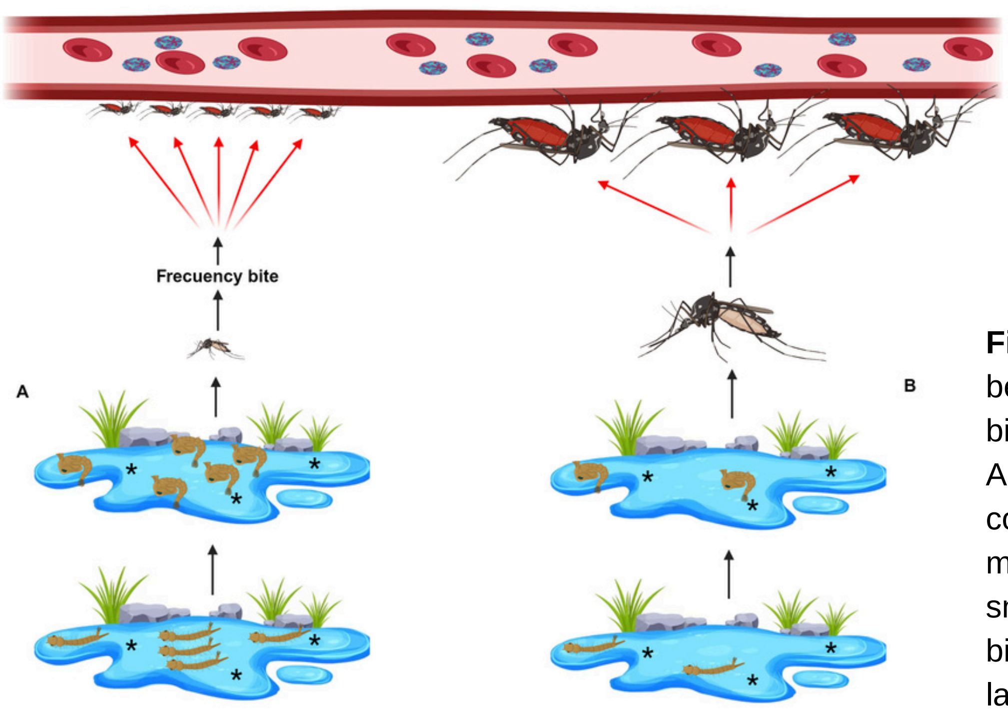

Figure 2. Relationship between body size and bite rate of *Aedes aegypti*. A, With increased larval competition, the emerging mosquito tends to be smaller and has a higher biting rate compared to larger mosquitoes (B).

be due to the availability and type of food (Braks et al., 2004; Gunathilaka et al., 2019), size of the container (Parker et al., 2019), or temperature (Jeffrey-Gutiérrez et al., 2020), which vary in certain space and time in natural environments. That is, asymmetric competition between two species could change to symmetric in specific periods mediated by biotic or abiotic factors and competitive measurements will only change in intensity (i.e., small or large adults under certain conditions).

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In larval habitats, another biotic factor that could mediate larval density and the competition thereof is predation (Fig. 1B). For example, the larviphage Mesocyclops aspericornis Daday, 1906 significantly affects larval mortality, development time, and pupal body weight of *Ae. aegypti,* with variations depending on initial larval density, nutrient supply, and temperature (Tuno et al., 2020).

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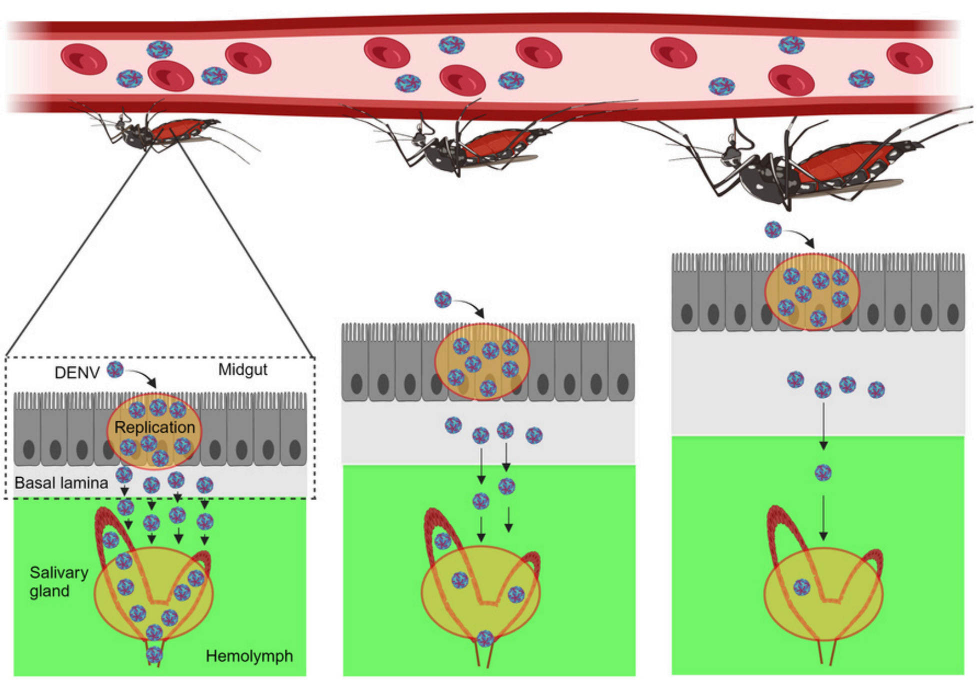

Figure 3. Hypothetical relationship between the size, basal lamina and vectorial capacity of the dengue virus in *Aedes aegypti*. The vectorial capacity decreases with respect to the increase in the size of the mosquito, which is correlated with the thickness of the basal lamina.

In terms of interspecific competition between *Ae. aegypti* and other species (not Culicidae) that coexist in water-filled containers, this is still uncertain; however, references in literature indicate that aquatic invertebrates such as ostracods and cladocerans compete for nutrients with *Ae. camptorhynchus* Thomson, 1869 and *Cx. pipiens* Linnaeus,1758 (Stav et al., 2005; Rowbottom et al., 2015).

Therefore, it is predictable to assume a similar result between *Ae. aegypti* and macroinvertebrates associated with their larval habitats (Fig.1C). Biodiversity and density of macroinvertebrate species (predators or competitors) could fluctuate differently throughout the year and geographic regions (Fierro et al., 2015), consequently heterogeneously impacting the competitive rates of *Ae. aegypti* (Fig. 1D); however, data to clearly answer these gaps are still lacking. In this context and in the absence of competition studies in regions where *Ae. aegypti* is established, it is important to ask which species coexist with *Ae. aegypti,* and what their relationship with the population dynamics of the species is?

In field studies, larval conditions can serve as a useful indicator of the nutritional structure of mosquito populations, as mentioned above, with the adult body size index playing a key role in this estimation, given that the effects of larval competition until adult emergence are well documented (Braks et al., 2004). In this context, measurements have focused on two main factors: adult and pupal mass, and wing length, with the latter being the most frequently used measurement in fieldwork (Juliano et al., 2014; Nasci, 1982).

Relationship of larval competition to Aedes aegypti adult behavior and life history

Body size of *Ae. aegypti* has been a robust negatively correlated indicator of competition among larval (Blackmore y Lord, 2000; Muturi et al., 2011). The estimation of this biological parameter has been studied under controlled conditions with field-collected and laboratory-reared strains and has been related to their behavior and life history, which are translated at the population level as fecundity, longevity, egg hatching, and biting rate (Blackmore y Lord, 2000; Alto et al., 2005; Juliano, 2009; Reiskind y Lounibos, 2009; Walsh et al., 2011; Qualls y Mullen, 2006; Braks et al., 2004; Alto y Juliano, 2001; Maciel-de-Freitas et al., 2007; Styer et al., 2007). In this context, it has been determined that females emerged from larvae under stressful conditions have a negative impact on blood intake, fecundity, and egg hatching rate (Alto et al., 2005; Juliano, 2009; Reiskind y Lounibos, 2009; Walsh et al., 2011; Qualls y Mullen, 2006), but their biting frequency increases (Lambrechts et al., 2011) (Fig. 2).

Because fecundity is determined as a function of the amount of blood ingested (Briegel, 1990; Xue et al., 1995), it is to be expected that smaller mosquitoes compensate for this biological function with an increased biting rate (Lambrechts et al., 2011). Regarding the longevity of *Ae. aegypti* adults, studies generally report that large adults emerging from favorable larval conditions have higher survival compared to adults emerging from stressful crowding (Reiskind y Lounibos, 2009; Alto et al., 2005) and this has been related to the biochemical composition of nutrients stored in the adult mosquito (e.g., glycogen, lipids, and proteins) (Alto et al., 2005). In disagreement, Joy et al. (2010) observed a negative association between body size and longevity.

The work done by Nasci (1986) informs us that in natural environments, large *Ae. aegypti* females may have a higher survival rate than smaller ones, and Juliano et al. (2014) observed in in vitro conditions that maximum longevity is established at a threshold of approximately 2.7 mm (wing length). However, nutrient composition and consequently longevity between different adult body sizes (small or large) could be compensated by food availability (sugar or blood intake) (Van-Handel, 1965). That is, in the absence of nutrients, smaller mosquitoes feed more frequently while larger mosquitoes feed less frequently because they have greater energy reserves (Nasci, 1986; Clements, 1999).

However, size thresholds that could be compensated for in longevity by the availability of food sources are unknown.

The behavior and life history of the adult mosquito are related to abiotic factors such as temperature and humidity, and possibly these conditions influence population dynamics. For example, it has been emphasized that *Ae. aegypti* oviposit higher numbers of eggs when exposed to 26ºC, as opposed to >30ºC (Blackmore y Lord, 2000). In extreme temperatures of 10°C and 35°C the movement of females is affected (Carrington et al., 2013), and this could have a direct impact on the behavior of this vector, such as the frequency of biting. Likewise, it has been reported that the longevity of *Ae. aegypti* adults, emerged from intraspecific and interspecific overcrowding with Ae. albopictus, is higher at 44% humidity compared to 77% (Alto et al., 2005). In addition, temperatures above 30°C increase the survival of adult mosquitoes (Blackmore y Lord, 2000).

Body size of Aedes aegypti and its relationship with DENV transmission capacity

Vector competence (VC) is the ability of a mosquito to acquire a pathogen by ingesting previously infected blood, develop infection and dissemination in secondary tissues, and infect a target host during subsequent contact (Christophers, 1960). The spread of DENV to the salivary glands is necessary for the mosquito to transmit the virus during the next blood feeding (Watts et al., 1987).

Body size of *Ae. aegypti* has been hypothesized to be indicative of DENV infection with conflicting results (Alto et al., 2008; Schneider et al., 2004; Lambrechts et al., 2006). Dissemination of DENV-2 in the adult mosquito has been observed to increase with smaller size, in the range of 2.0-3.8 mm [wing length (Alto et al., 2008)], while Kang et al. (2009) indicate that large mosquitoes emerging from optimal larval crowds are more proficient in disseminating DENV-2. However, the comparison between the two studies hardly reaches a consensus due to the methodological heterogeneity, such as mosquito strain, time of exposure to the virus, and temperature, which are important variants in the viral infection of *Ae. aegypti* (Lambrechts et al., 2006).

The complexity in determining the biological processes involved in adult mosquito susceptibility to infection and transmission of DENV has led to the proposal of different hypotheses such as competition-longevity, which indicates that susceptibility to infection and eventual transmission is determined primarily by adult survival, and physiological processes become secondary (Alto et al., 2008; Juliano et al., 2014).

Studies using viral detections directly from field-collected adult mosquitoes [Brazil (Juliano et al., 2014)] and in vitro nfections of adults emerging from larvae collected at different sites in Thailand reinforce the hypothesis that the frequency of DENV infection increases prospectively with the size of the *Ae. aegypti* female (Sumanochitrapon et al., 1998). However, transmission capacity may be compromised mainly with longevity, which seems to have a maximum value at an intermediate size (2.7 mm), according to the study by Juliano et al. (2014).

The thickness of the basal lamina in the midgut has a positive relationship with mosquito size and this characteristic has been related to LaCrosse virus (LACV) infection in Ae. triseriatus (Grimstad y Walker, 1991). The basal lamina is a barrier that can prevent the escape of the virus into the hemolymph and its dissemination in different tissues, including the salivary glands; therefore, the lesser the thickness, the greater the probability of infection, dissemination, and eventual viral transmission (Grimstad y Walker, 1991). Although these processes in the *Ae. aegypti*-DENV interaction are not clear, it is possible that they explain variations in susceptibility to infection at different body sizes (Fig. 3).

An approach to DENV transmission responses is likely to be found in work on temporal fluctuations of *Ae. aegypti* and dengue epidemiology. It has generally been proposed that mosquito density increases the risk of viral transmission (Scott et al., 2000); however, different studies have not related vector variables to DENV transmission in the human population (Gubler, 1998; Lambrechts et al., 2011). Although the answers to these controversies are still difficult to elucidate, it is likely that, during periods of high dengue incidence which have a homogeneous pattern in different endemic areas (Kyle y Harris, 2008), mosquitoes with highly competent body sizes are involved in viral transmission, mediated by biotic and abiotic factors in a time and space in dengue endemic areas (Fig. 1D).

These mosquitoes may not necessarily have highly long-lived or susceptible body sizes, but rather body sizes that are sufficiently susceptible to viral infection and spread, as well as sufficiently long-lived for DENV transmission (competence-susceptibility-longevity).

In the absence of concise evidence and a consensus by the scientific community in determining the processes related to the epidemiological fluctuation of dengue in endemic areas, it is important to monitor the fluctuation of adult sizes and their relationship with DENV transmission, in order to establish body sizes highly competent in viral transmission and establish vector control measures focused on determining body size thresholds with low probability of infection. A rigorous evaluation of this proposal is important to develop evidence-based dengue control strategies.

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