Chapter

The Yellow Fever Mosquito *Aedes aegypti* (Linnaeus): The Breeding Sites

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Abstract

Important information about yellow fever mosquito *Aedes aegypti* (Diptera: Culicidae) and the identification and quantification of the main Brazilian breeding sites for this vector are highlighted in this chapter. Although most of the control actions have been directed to the adult (winged) phase of the vector, the reduction of immature forms (eggs and larvae) of *Aedes* is the most important way to control these insects, especially to eliminate breeding sites. These are, in principle, the most important targets for mosquito population control in order to reduce infestation and, consequently, the transmission and incidence of diseases transmitted by insect vectors. Thus, this chapter presents a compilation and discussion that allows comparing characteristics and similarities of *Aedes* species.

Keywords: mosquito vectors, population control, *Aedes aegypti*, dengue, public health

1. Introduction

Mosquitoes in the family Culicidae are responsible for the transmission of viruses and other pathogens to man and animals. Arboviruses transmitted by mosquitoes of the genus *Aedes* (Meigen) (Diptera: Culicidae) promote the occurrence of diseases such as dengue fever, chikungunya fever, yellow fever and zika fever at alarming levels and have impacted public health in several countries, mainly Brazil [1, 2].

In Brazil, there is an outbreak of wild yellow fever [3] due to virus transmission, which should be kept in the wild, between non-human primates and arboreal wild mosquitoes, mainly of the genera *Haemagogus* (Linnaeus) (Diptera: Culicidae) and *Sabethes* (Robineau-Desvoidy) (Diptera: Culicidae). The possibility of a change in the ongoing yellow fever transmission cycle has been realized. To date, it has not been proven that the yellow fever mosquito *Aedes aegypti* (Linnaeus) (Diptera: Culicidae) mosquito is involved in transmission, but evidence has emerged from different studies [3].

With the exception of yellow fever and dengue, zika and chikungunya do not have specific vaccines or treatments. For this reason, the use of insecticides and chemical control constitutes the main insect vector control tools in urban areas. However, this practice has been disseminated and performed irresponsibly, resulting in actions that caused resistance to these insecticides. In this respect, new forms of control are desirable, especially with multifunctional products [3].

In Brazil, *Ae. aegypti* is found in more than 70% of the 5561 Brazilian municipalities. Most of these areas have a reduced number of health agents who, for different reasons, do not cover 80% of cities' urban areas. Thus, the country is left exposed to constant threats of outbreaks and epidemics. Thereby, it is necessary to develop new products, methodologies or even a combination of methods to control *Aedes* spp., populations. These methods should take into account effective surveillance and control, and be of a low cost and easy applicability. Additionally, efforts to improve infrastructure, population education, and training of health workers to combat and control the insect should be intensified. To this end, a better understanding of the different aspects of Culicidae biology and diversity, their relationships with humans and animals, and their reproduction in urban areas are important factors in assessing the adequacy of methodologies used for the selection and implementation of control methods, the development of new insecticides or the creation of new strategies that consider behavioral and adaptive aspects. However, information, techniques and/or scientific knowledge are still restricted to the majority of the population or have limited practical applications. It is up to the universities, research centers and zoonotic control agencies to obtain them and use the contents for discussion or establishment of new proposals and strategies of vector population control.

In this context, it is very useful to present a review of breeding sites, habits and behaviors of the *Aedes* species to understand the situations, conditions and/or details of the microenvironments, and reproduction at breeding sites, whether natural or artificial. Thus, this chapter is based on the collection and analysis of information available in the literature, or the authors' scientific experience, about the physicochemical and biological conditions of breeding sites and mosquito habits and behaviors. Considering these important findings will crucially enable the elaboration of strategies that control insect vector populations.

2. Reproductive cycle, behaviors and habitats

Mosquitoes use the aquatic environment to develop immature forms (egg, larva and pupa). In urban and peri-urban environments, breeding sites are any artificial reservoirs or containers and even natural breeding grounds where water is available for the reproductive process of the species. The availability of breeding sites and feeding facilities explains, in part, the spread of *Aedes* spp. *Ae. aegypti* is considered the main vector of (re)emerging diseases in Brazil (yellow fever, dengue, chikungunya and zika) and has been a constant concern for public health.

The genus *Aedes* [including *Ae. aegypti* and Asian tiger mosquito *Aedes albopictus* (Skuse) (Diptera: Culicidae)] has peculiar habits in relation to other mosquito species. The species oviposit in a split way, usually in aquatic environments with areas of restricted lighting or shaded spaces. At these locations, temperatures are milder compared to an area of direct solar sunshine. Shaded spaces and the availability of organic debris are physical and chemical signs that the breeding facility was suitable for previous generations and can successfully serve the breeding of a new generation [4].

Breeding sites are important spaces for the attraction, reproduction, survival guarantee and continuation of the species. These microenvironments are determinants for oviposition and reproductive success. Food availability in the aquatic environment appears to be the main attraction for oviposition, along with the physicochemical and biological conditions of the breeding sites. These related aspects can all influence the choice of the oviposition site by the females.

The abundance and population density of mosquitoes produce negative impacts on the quality of life of humans and animals. Diseases caused by arthropod-borne arboviruses are considered as neglected or emerging diseases. Viral diseases transmitted by *Aedes* spp., including yellow fever, dengue fever, chikungunya and zika, are serious public health problems that persist for decades in the form of periodic outbreaks with variable intensities due to non-continuous and deficient control methods. Since the early 1970s, the World Health Organization (WHO) has sought an effective way to control, manage and treat these diseases, but without much success.

Ae. aegypti undergoes four stages in its life cycle (**Figure 1**): egg (terrestrial form), larva, pupa (aquatic forms) and adult insect (winged; terrestrial form). Despite having a short shelf-life of at most 2 months in the laboratory (and less time in natural environments), the female can oviposit up to 270 eggs during her life span. As a strategy for species survival, egg laying and establishing an egg bank at breeding sites allows the maintenance, replacement and perpetuation of the species even under adverse conditions [5]. Split oviposition at the breeding sites performed by *Ae. aegypti* and *Ae. albopictus* allows them to increase survival conditions and establish the population in the ecosystem.

Rozeboom et al. [6] observed that females disperse their eggs through several breeding sites. In each site, 11–30 eggs are deposited by oviposition in small breeding sites and more than 60 eggs in large breeding sites [7]. Vector control strategies should include knowledge about the reproductive aspects of the insect due to the formation of an egg bank that allows for species reposition in the environment. Studies showed that both preferences and habits, as well as insect survival strategies, are important factors that must be considered by the vector control agent [7, 8].

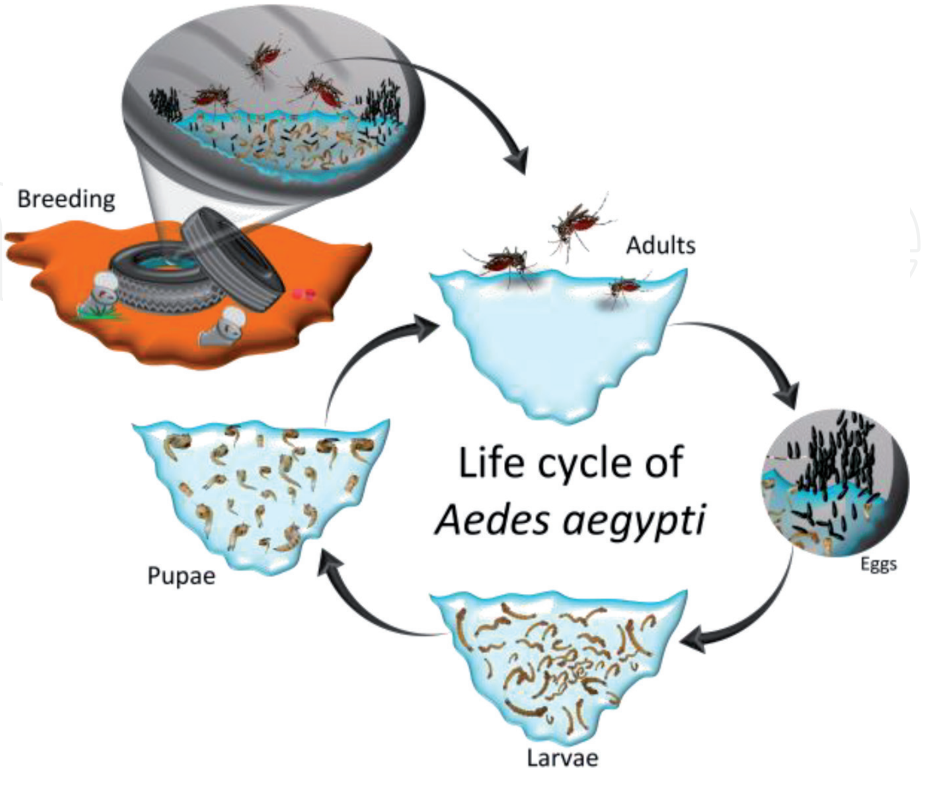

Figure 1.
Life cycle of Aedes aegypti *(Linnaeus) (Diptera: Culicidae).*

The literature mentions that the breeding site must be viable for reproduction of the species, with food availability and adequate oxygenation, temperature and pH. The choice of oviposition sites is a critical factor for the survival and dynamics of populations, and knowledge of these factors is important for mosquito population control. The choice of such sites results in a complex interaction between chemical and physical factors (biotic and abiotic), which indicates the degree of preference in the selection of breeding and oviposition sites [4–9]. Laboratory studies done by Madeira et al. [10] showed *Ae. aegypti* preferences for some types of breeding grounds. There are variations in the type of breeding sites chosen by this species for oviposition. Oviposition can occur in the water when the egg-laying surface does not allow egg adhesion. Non-submerged eggs usually do not hatch, in contrast to submerged eggs that hatch after hydration stimulation. Mosquitoes prefer porous or rough surfaces for oviposition.

Mitchell-Foster et al. [11] showed that new strategies can be used for integrated vector control. The imposition of unfavorable conditions for insects at breeding sites can help to increase insecticide effectiveness and vector control, since insecticides can be multifunctional for comprehensive secondary or tertiary control, due to changes in breeding sites physicochemical and/or microbiological conditions. These strategies could be integrated to consider applying disadvantageous situations and they include biological agents at different levels for *in situ* reproduction control. Exposure to competitors, physicochemical changes and others reduce the probability of egg hatching and species survival, besides affecting parameters such as larval maturation time, adult size, population density, fecundity, attraction and egg viability.

Rey and O'Connell [12] investigated *Ae. aegypti* and *Ae. albopictus* oviposition behavior by examining oviposition site characteristics and the influence of factors that alter egg laying. In cages, they prepared several combinations with females of both species for oviposition at breeding sites in vegetation (potted plants) or structural components (blocks of wood and concrete). Then they compared the number of eggs deposited per female among the species and the different types of breeding sites. *Ae. aegypti* deposited more eggs per female in breeding sites with vegetation compared to those with structural elements. The opposite is true for *Ae. albopictus*. *Ae. aegypti* females presented a higher oviposition frequency than *Ae. albopictus*. On average, 63% of breeding sites contained eggs from both species. The authors emphasized the possibilities of interactions between *Ae. aegypti* and *Ae. albopictus* in spaces and breeding grounds, especially when the two species are disseminated in the same space where specific interactions and mechanisms must contribute to reproductive cooperation.

After oviposition on the breeding walls, white eggs in the posture darken on contact with atmospheric oxygen. Eggs are deposited on the walls of the breeding site when the surfaces are porous or rough and close to the water surface (but not directly over the liquid when there is this availability of an oviposition surface). Humidity must be maintained for egg viability and hatching after submersion/hydration in water. Studies revealed that these eggs can survive 360–450 days after desiccation. Under favorable conditions, their hatching can occur between 10 minutes and 48 hours after humidification or immersion in breeding liquids, and after 7–10 days, they emerge as adult insects with vector potential, depending on the temperature and available feeding conditions [13, 14].

Mosquitoes seek shelter, dark spaces with microbiota and decomposing organic wastes available over a wide pH range (acidic, neutral and basic). If the insect does not find these conditions, it will look for other places, regardless of the size or condition, for their reproduction. The insect will never put all its eggs in a single breeding site. This survival strategy led to marked reproductive success and greater dispersion, features that make the mosquito resilient, competent and adapted to the different conditions offered by the medium for its survival, despite its apparent fragility. Its adaptive and vectoral capacities underscore its epidemic potential due to the ability to spread across different geographical areas [15].

After hydration and egg hatching, the larval stage begins, which has four evolutionary steps. Its duration depends on temperature, food availability (organic material or microorganisms) and number of larvae in the breeding site. Under these conditions, the period between hatching and the pupa (last stage before the adult insect) may not exceed 5 days. However, if there is low temperature and food shortage, the stage can be extended for up to a week [14].

The *Ae. aegypti* larva is composed of a head, thorax and abdomen. The abdomen is divided into eight segments. The posterior and anal segment of the abdomen has four lobulated bronchi for osmotic regulation and a siphon or air tube for breathing on the water surface. The siphon is short, thick and darker than the body. To breathe, the larva goes to the surface, where it is in almost vertical position. It moves in the shape of a serpent, making an "S" in its displacement. It is sensitive to sudden movements in the water and under a beam of light, it moves quickly, seeking refuge at the bottom of the vessel. This behavior is more related to antipredation because females select the oviposition site based on the success of previous generations as well as the presence of decomposing organic debris [4].

The pupae do not feed and at this stage metamorphosis of the larval stage occurs to generate the adult (winged) insect. This stage lasts 2–3 days and when the pupa is inactive it stays floating on the water surface to facilitate the emergence of the adult (winged) insect. The pupa is divided into the cephalothorax and abdomen. The head and thorax are united and constitute the cephalothorax, which gives the pupa, seen from the side, the appearance of a comma. The pupa has a pair of breathing tubes or "trumpets" that cross the water and allow it to breathe [14, 15].

The adult phase of the insect represents the reproductive and transmitter/vector phase. The adult is responsible for the spread of viruses and diseases and for the reproduction. *Ae. aegypti* is approximately 1 cm long and have black with white stripes distributed near the body and legs. *Ae. aegypti* incidence is usually greater in spaces with high temperature, low humidity, low vegetation and a concentration of heat sources. Unlike common mosquitoes, *Ae. aegypti* has diurnal habits, flies low and performs hematophagy, preferentially stinging the feet, ankles, arms and legs. *Ae. aegypti* does not like heat or radiated/lighted environments, so it is more active in the early morning and late afternoon. It is believed that the environment in these adverse conditions of irradiation and/or competitiveness with other species is more aggressive for the adult mosquito, which imposes an additional metabolic cost to its survival. The female feeds on blood (hematophagy), which is a ready and metabolized food source that is still rich in proteins, and minerals along with other micronutrients necessary for its survival, oviposition and the maintenance of its vector competence. However, the female only transmits a virus if she contracted it more than 2 weeks ago, since the dengue virus needs 10–14 days in mosquito metabolism to become viable for transmission during hematophagy [16].

2.1 The breeding sites of *Aedes*

The availability of different types of discarded containers with organic remains allows rainwater containment. Maintaining these conditions for a certain period of time allows the formation of new breeding sites that attract females for oviposition and ultimately promotes Aedes larval infestation.

Reproductive habitat characteristics may affect larval population density. Thus, the mosquito will be more abundant and the potential for disease transmission will increase. In this situation, quality of life is deeply affected by vector diseases, especially for individuals who live in high-population-density areas where disease will be transmitted more quickly.

Getachew et al. [17] showed the importance of basic sanitation and the simple treatment of water with chlorine, which represents an important control for the restriction of disease outbreaks. In containers that contain tap water, mosquito larvae are not abundant, contrary to what happens in containers filled with a mixture of tap water and rainwater or only rainwater. De Brito-Arduíno and Ávila [18] researched and discussed the reproduction and characteristics of urban breeding sites, and the implications for *Ae. aegypti* and *Ae. albopictus* control. The authors' results corroborate studies performed in Australia, where 28% of immature individuals came from tanks and wells, considered to be the main breeding sites [19]. Other studies performed in Venezuelan cemeteries showed that the breeding sites with the highest proportion of pupae have been those that containing 1–5 liters of liquid [20]. Additionally, the results presented great variability in the parameters, since immature individuals of *Aedes* spp., occur in water with pollutant load [19].

The species can develop in breeding grounds with a high degree of pollution and organic matter. The polluted breeding sites found in De Brito-Arduino and Ávila's studies [18] are boats, drains and sites that contained the residues of various substances, such as oil, salt, rust, among others [21]. In studies performed in Puerto Rico, a large number of *Ae. aegypti* larvae grew in tanks and septic tanks, cooperatively with *Culex quinquefasciatus* (Say) (Diptera: Culicidae) populations [22, 23]. In Brazil, laboratory analysis showed that *Ae. aegypti* can complete its reproductive cycle up to the adult (winged insect) phase in waters with different degrees of pollution [21–24]. In Merida, Mexico, the main *Ae. aegypti* breeding sites are composed of rainwater runoff from the streets and localities that have a high pollutant load [25].

Ae. aegypti prefers breeding sites with high food availability when there are no conspecifics (*Ae. albopictus),* while *Ae. albopictus* prefers high food availability when larval density is relatively low [25, 26]. The literature suggests that *Ae. aegypti* possesses the ability, genetics and competence to adapt and survive in different biotic and abiotic conditions that result from anthropogenic changes. Studies revealed that larvae and pupae are found in breeding grounds with water of different quality and portability. Some breeding sites contain residues of different substances, as well as different temperatures, pH, dissolved oxygen (DO) and conductivity. These results demonstrate that the species can survive in non-conventional breeding sites [27–29].

Taken together, these facts highlight the challenge for mosquito population control and the reduction of viral disease incidence in urban and peri-urban environments. Effective *Ae. aegypti* population control to reduce disease incidence should focus on multifactorial strategies and take into account the different physicochemical and biological aspects of breeding sites.

2.2 Physical-chemical characteristics of breeding sites

The physicochemical characteristics of aquatic habitats influence the survival rate of mosquitoes [15–17]. Some factors may be important for mosquito oviposition, including water temperature, pH, ammonia, nitrate, sulfate and phosphate content, conductivity and dissolved solids [30, 31].

Following oviposition on the breeding wall, eggs hatch after hydration, and the insects develop through the four larval stages and pupa (which does not feed) until adulthood. The immature stages, namely eggs and larvae, are important parts to consider in population control. From egg hatching (embryo), the larvae consume decomposing organic material, debris and microorganisms from the aquatic microenvironment to obtain nutrients for their development, which are actions that contribute to reproductive cycle closure. These aspects can and should be considered for the establishment of new insecticides, formulations and strategies for insect population control. Control via the food chain, studies on microbiota composition (including prevalent and non-prevalent species), mosquito characteristics and specificities, the attractiveness of the breeding grounds to females and other details are important considerations to develop products and strategies for target species population reduction. Current research reveals that the type of container, water quality and the available physical, chemical, biological and nutritional conditions found at the breeding microenvironment are important parameters for the attraction, reproduction and continuation of the species. Thus, these factors are likely imperative for population control.

According to the historical incidence of vector-borne diseases, infection peaks occur during hot and rainy seasons. At these times, water storage lasts for prolonged periods, with the potent combination of humidity, temperature and food availability. The hot and humid climate increases mosquito population density from these breeding grounds, food and conditions favorable for reproduction of *Aedes* spp., all of which increase the risk of the incidence of the different diseases transmitted by them [17].

Studies in Africa, Asia and various parts of the world indicate that the predominance of *Aedes* spp. (*Ae. aegypti* and *Ae. albopictus*) in a given region depends on the climatic conditions, type of breeding grounds and form of species dispersal. The use of abiotic parameters like water conductivity (salt dispersion/electrolytes) as an index for mosquito proliferation in garbage dumps can be explored in mosquito control strategies [30].

Getachew et al. [17] observed that water conductivity in the range of 162.9–616.9 $\mu S\ cm^{-1}$ negatively correlates with larval density. Fillinger et al. [32] also showed a negative correlation of larval density to malaria vector. A conductivity of 2000 $\mu S\ cm^{-1}$ significantly reduces larval density at breeding sites. The authors also showed that the breeding site pH ranged from 6.72 to 7.63, with a positive correlation with larval density.

Breeding site ionic composition and pH are limiting factors for the distribution and number of organisms found in these habitats. However, Clark et al. [33] showed that the mosquito has a high adaptation capacity to the breeding site conditions. *Aedes* spp. can develop in extreme pH (4.3–9.9), wide temperature ranges (18–35.9°C) and different salinity levels. The insects prefer environments with leaves and decomposing organic material, although it is not an absolute rule for *Aedes* spp., with reproduction capacity in waters polluted by oil, salt and rust, among other factors. Indeed, De Brito-Arduino and Ávila [18] observed breeding sites in boats with motor oil residues, data that may also justify the minimum dissolved oxygen (DO) value of 0.40 $mg\ L^{-1}$. The drains also had low DO (0.20–0.52 $mg\ L^{-1}$) in the various collected samples, besides the presence of soap residue and detergents that would justify these DO values.

Another factor that influences the choice of breeding sites is salinity. Oviposition decreases with increasing salinity at concentrations above 12% [17, 30, 32, 34]. De Brito-Arduíno and Ávila [18] showed that these limits are flexible, with salinity values up to 13.5%. Increases in conductivity (salinity) impose unfavorable conditions for oviposition [18, 35]. In the littoral strip of Brazil and Asia, there are records of *Ae. aegypti* reproducing in water with high salinity (brackish water), data that demonstrate the existence of the species adaptation to the salinity of the breeding sites [21, 24].

Another study showed that breeding sites can be shared by different species for survival at different pH ranges. *Ae. aegypti* and *Cx. quinquefasciatus* (common stilt) have been found in breeding sites with pH in the range of 6.5–8 [36]. Brito-Arduino and Ávila [18] also observed that the breeding pH range varies from acidic to basic, with values from 4.3 to 9.9. These results are related to other studies performed in Australia, which showed a breeding site pH range of 5.5–11.3 [37], and in Venezuela, with pH between 6.5 and 10.5 [20]. Since the hydrogen ion concentration [38] is dependent on the water containment medium (breeding sites) and temperature, due to the water ionization constant, temperature is another factor that deserves careful analysis.

Temperature influences the immature development of *Ae. aegypti*, and thus, the availability of energy from the medium may interfere with metabolic activity, but mainly with the enzymatic activities of the organism. High temperatures can compromise the conformation, stability and function of insect metabolic enzymes, as well as activate and deactivate them or even alter metabolic processes that are involved in the development, adaptability and survival of these organisms [33, 37, 39]. As previously stated, the species can successfully develop and breed between 18 and 35.9°C [18]. Studies performed in Colombia revealed that *Ae. aegypti* larvae could grow from 24 to 30°C at breeding sites [39, 40]. Another related study conducted in Nukulaelae (Tuvulu), with breeding grounds in metal/plastic drums, showed that *Ae. aegypti* occur in environments with temperatures between 20 and 35°C [41]. The pH and salinity may limit the distribution of organisms. However, they cannot prevent reproduction under unfavorable abiotic conditions. The conductivity (salinity) of the water in the breeding sites of De Brito-Arduíno and Ávila [18] study, ranged from 0 to 22,400 μS cm^{-1} (0–13.5% salinity) and pH from 4.5 to 9.9 (depending on the collection and type of breeding sites). These results suggest that *Ae. aegypti* can reproduce under unfavorable conditions and thus overcome limiting factors for species development in extreme temperature, pH, DO and conductivity conditions.

In a study conducted by Rao et al. [30] in *Ae. albopictus* breeding sites, there is a positive correlation between larval density and total dissolved solids, turbidity, conductivity and salinity, and a negative correlation for pH. Dom et al. [42] and Nazri et al. [43] showed the potential risk of mosquito peri-domiciliary establishment and the characteristics of the breeding sites for *Aedes* spp. *Ae. albopictus* is the predominant species in breeding sites. Turbidity, pH, total organic carbon (TOC), magnesium, calcium and sodium are among the characteristics that are positively significant for larval density, species composition and breeding water characteristics, respectively. Mosquito breeding sites characteristics affect larval density and increase mosquito infestation, which ultimately impact the quality of life of the population.

Breeding characteristics play an important role in providing nutrients and a safe environment for increasing the larval survival rate. Different studies showed that turbidity (due to the presence of organic material and microorganisms), pH, TOC and magnesium concentration influence the larval population density. *Ae. aegypti* prefers less turbid water, while *Ae. albopictus* prefers more turbid water. These differences may indicate why one species prevails over another. The results suggest that *Ae. aegypti* is a less-demanding species in terms of food for oviposition and reproduction.

TOC, related to the presence of organic material in breeding sites, also influences larval density. This fact has been confirmed by a study of Thangamathi et al. [44], which indicated that sulfate ion (SO_4^{-2}) content in the breeding habitat of *Aedes* larvae (*Ae. aegypti* and *Ae. albopictus*) is high compared to other ionic species. *Aedes* spp. have a rapid adaptation capacity to environmental conditions, even if they appear to be averse to the species. According to Thangamathi et al. [44], *Ae. aegypti* survives most at pH between 6.5 and 8.0; however, values close to neutrality are better for the species [45]. This pH range may be altered to affect species adaptation and potentially to control the population.

Micro and macro nutrients availability in breeding sites is also important for *Ae. aegypti* and *Ae. albopictus*. Magnesium plays a role in larval density, as shown by Thangamathi et al. [44], who carried out studies that analyzed breeding site mineral composition. Calcium, potassium, sodium, sulfur (elemental or SO_4^{-2}) and magnesium [2] can provide an ideal broth for *Ae. aegypti*. The larval habitat characteristics have been analyzed and related to the species by larval number. Calcium and sodium provide significantly different results for the proposed composition that favors *Aedes* spp. in breeding sites.

These results show that any container that can store water for a prolonged period for domestic or industrial use becomes a potential mosquito breeding ground, since it can allow the deposition of minerals and organic material, colonization by microalgae and microorganisms, and thus gather conditions for the development of a microenvironment favorable to the life and reproduction of *Aedes* spp. In this regard, strategies such as insecticides or other products could potentially change breeding site physicochemical parameters in terms of pH, conductivity and nutrient availability for secondary vector control (due to reproductive microenvironment changes).

2.3 Attractiveness of females to breeding sites

The *Ae. aegypti* oviposition strategy differs from other mosquito species. The literature shows that the oviposition stimulus is mainly food availability, signaled by microbiota semiochemicals that result from the degradation of organic materials and/or microorganisms. Semiochemicals are signaling molecules, used to carry information between living organisms that cause changes in *Ae. aegypti* behavior. These semiochemicals are perceived by the female, stimulate oviposition and consequently, allow species continuation, possibly because they indicate food availability for the larvae.

There are few studies that relate the attractiveness, selectivity and the relationship between microorganisms (i.e., bacteria) and products of organic degradation of breeding sites for attraction and oviposition. The available reports pay little attention to the density and colonization of breeding grounds by bacteria and other organisms and the female's attraction or repulsion and oviposition. Hasselschwert and Rockett [46] examined *Culex* larvae growth at breeding sites with different bacterial cultures and observed that the presence of *Bacillus cereus* and *Pseudomonas aeruginosa* induces attraction for *Ae. aegypti* oviposition. Trexler et al. [47] showed that isolates of *Sphingobacterium multivorum* (Sphingobacteriales: Sphingobacteriaceae), *Psychrobacter immobilis* (Juni and Heym) (Pseudomonadales: Moraxellaceae) and an unidentified *Bacillus* (Cohn) (Bacillales: Bacillaceae) species, when inoculated in water, induce high *Ae. albopictus* attraction and oviposition compared to water without these bacteria [40]. Poonam et al. [48] produced filtrates from bacterial cultures and used them for analysis of attraction and oviposition with female *Cx. quinquefasciatus*. These females oviposited more in certain concentrations of *B. cereus* (Frankland and Frankland), *Bacillus thuringiensis* (Berliner) and *Pseudomonas fluorescens* (Flügge) (Pseudomonadales: Pseudomonadaceae) compared to tap water. Other filtrates from *Bacillus megaterium* (Bary) and *Azospirillum brasilense* (Tarrand, Krieg and Döbereiner) (Rhodospirillales: Rhodospirillaceae) did not stimulate oviposition in water at any concentration of the filtrate tested. These results demonstrate that there is selectivity in the attraction and response of the mosquito to different bacteria. Bacteria grown in disparate nutritional media and this medium is not used as a control because it may contain substances that are attractive or deterrents for oviposition.

Huang et al. [49], in a study with 14 isolates of bamboo leaf infusion bacteria, showed that *Ae. aegypti* are repelled at densities of 109 cells mL^{-1}. The mixture of 14 bacterial isolates attracts *Ae. aegypti* and *Ae. albopictus* at densities of 107–108 cells mL^{-1}. These studies showed a concentration range dependence of 106–109 cells mL^{-1} for *Aedes* spp. attraction. *Ae. aegypti* and *Ae. albopictus* females are attracted by an infusion of bamboo leaves and a mixture of 14 bacterial species [50–52]. The results indicate that volatile substances from plants or bacteria can be attractive to mosquitoes. Despite the differences in the responses of *Ae. aegypti* and *Ae. albopictus* to different bacterial concentrations and densities, *Ae. aegypti* females tend to be attracted to lower bacterial concentrations and densities compared to *Ae. albopictus* females.

Other data available in the literature indicate that not all bacterial species produce the same semiochemicals (attractive or repellent) or sufficient amounts of attractants. These results suggest that there is a possible biological balance in the microbiota that controls, from the population density of the present species, the emission of volatile substances that can be perceived by the females in the process of attraction or repulsion to the breeding sites. Semiochemical composition variations from different bacterial species that stimulate the attraction or repulsion and oviposition of *Aedes* spp. explain the different species response. Further, other parameters, including variations in bacterial production time, can promote quantitative or qualitative differences for the chemical stimulus in the process of attraction or repulsion to the breeding sites and humans skins emanations [49, 53]. Thorn et al. [54] described significant differences in the type and concentration of volatiles produced by different bacteria grown in the laboratory and in nature for oviposition [6]. Ponnusamy et al. [50] showed the complexity of a microbiota balance and its importance in breeding sites for mosquito breeding. Their studies reinforce the hypothesis that the main stimulus for female ovipositors is the availability of food indicators or breeding site microbiota.

2.4 Perspectives of integrated pest management (IPM) applied to population control of vectors

Diseases transmitted by *Ae. aegypti* are one of the major public health problems in many regions of the world; hence, their control is import. Thousands of years of natural selection increased vectoral competence and even species survival to the cultural habits of populations/communities. Additionally, lack of health education, high availability of breeding sites in domiciles and peri-domestic areas, and the absence in many places of sanitary infrastructure, among other factors, contribute to increase the survival and reproduction success of mosquito species and prevent their population control.

Despite of reports and dissemination of the polyvalent vaccine for dengue, chikungunya and zika that may be an option to reduce and control these diseases, this use can take up to 10 years for successful control, according to the Oswaldo Cruz Foundation (Fiocruz, RJ), due to the conditions required to guarantee efficiency and biosafety. There are four dengue serotypes and the number of serotypes for the other two viruses is still unknown, and must also be combated efficiently. For this reason, there is enormous dependence on chemical control and the need for eliminating *Ae. aegypti* breeding sites to reduce the mosquito population and consequently, the incidence of the diseases. The vaccine may be an important part for dengue control; however, other fronts should also be considered, such as health education, continuous epidemiological surveillance, infrastructure improvements and social responsibility by governments.

2.4.1 Mechanisms of resistance to chemical insecticides

Chemical methods are intensively used for adult insect vector population control. Non-implementation of preventive control strategies is in part, responsible for the occurrence and constant aggravation of epidemic outbreaks during hot periods in Brazil.

The difficulty for *Ae. aegypti* population control centers are on the adaptive process, species resilience and acquired resistance to conventional insecticides. The first report of resistance occurred with organophosphates followed by pyrethroids. Over time, other resistance records have been reported to organophosphates, pyrethroids and carbamates in regions with intense mosquito occurrence. Before the year 2000, resistance to the organophosphate insecticides Temephos used as a larvicide and Malathion used to combat adult mosquitoes, was detected in some Brazilian municipalities.

Reproductive capacity favors the emergence of insecticide-resistant individuals used for vector control, because resistance varies with the time of use and concentration of the products that act at specific sites of toxicity. Medeiros [55] presents four categories of enzymatic activity profiles: (1) greater activities in the adult stage; (2) greater activities in the larval stage (esterases "α-EST" and "β-EST"); (3) activities that increase during each stage evaluated (mixed function oxidase [MFO]); and (4) activities that tend to increase in the larval stage and decrease in the first days of adult life (DVA) [esterase "ρNPA" and glutathione S-transferase (GST)]. Biochemical assays with larvae and adults from field populations revealed alterations in acetylcholine esterase (AChE) and other esterases at the larval stage, changes in GST more restricted to the adult stage, and MFO alterations have been limited to the two vector stages.

The results from these experiments allow detailed evaluation of the resistance mechanisms in different vector populations and can be used for the development and choice of insecticides more suitable for *Aedes* spp. control. Guirado and Bicudo [56] showed some aspects of population control and resistance to insecticides in *Ae. aegypti* and concluded that mosquito population control, as long as no more modern vaccines or genetic techniques of epidemiological control are available, is exclusively dependent on chemical control and human population awareness for breeding site elimination.

The available insecticide resistance studies demonstrate that resistance is due to three main mechanisms: (a) reduction of insecticide penetration due to changes in the insect cuticle; (b) increased metabolism of the insecticide by the action of esterases, mono-oxygenases or glutathione-transferases that inactivate the molecule; and (c) modification of the insecticide's biological target. The literature also shows a behavioral resistance mechanism, where insects avoid contact with sites that contain the toxic substance used for control. The results of insecticide resistance and loss of control efficacy indicate the need for continuous monitoring of *Ae. aegypti* susceptibility to insecticides and the use of chemical control in more rational ways. These smarter considerations include analysis of insect populations and their resistance, use of integrated management techniques and different methodologies and/or control products, in addition to continuous monitoring during all periods of the year by endemic control programs.

2.5 Attractiveness to breeding sites from water quality

The availability of water by precipitation or accumulation at home and breeding grounds is an important factor for the reproductive process and establishment of

Aedes spp. [57, 58]. Additionally, food availability is the most important factor for larval survival and development. Researchers have analyzed breeding site physicochemical conditions and water parameters. The studies reveal species adaptations and tolerance to the physicochemical conditions of breeding sites, besides the presence of other species that share breeding site spaces and cooperate with each other. Gil et al. [29], through collection and analysis of breeding water, showed a close relationship between the conditions of drinking and non-potable water composition, temperature, availability of organic material, waste, and reproduction and development of *Ae. aegypti*. Beserra et al. [26] showed that *Ae. aegypti* develops in different environments with organic material availability. The temperature, pH and water composition (total solids, total nitrogen, ammoniacal nitrogen, total dissolved phosphate and DO) are important variables for *Ae. aegypti* reproduction at egg, larval and pupal stages.

Silva and Silva [59] studied the influence of egg quiescence (interruption in development induced by low humidity) period in the life cycle of *Ae. aegypti* under laboratory conditions, in search of information that could improve control actions. Notably, the egg is the most resistant form of the biological cycle, and this feature allows mosquito development and resistance to climatic adversities. The experiments have been performed in a biological chamber, maintained at 28 ± 1°C, with relative humidity of 80 ± 5% and a 12-hour photoperiod. Quiescence is highly significant for larval hatching. Eggs from the same quiescence period had statistically different incubation periods and the larvae hatched in groups (defined by incubation). Indeed, in 99.8% of the cycles, the variation was determined by incubation.

Quiescence is a very important adaptation in the passive dispersion of *Ae. aegypti* because it enables the transport of resistant (or quiescent) eggs into all kinds of artifacts, such as used tires. Its non-destruction can signal a feasible mechanism to increase *Ae. aegypti* dispersion, a factor that makes entomological and/or epidemiological surveillance essential. This context gains another dimension when one adds the highly significant effect of quiescence on larval hatching. Quiescence periods of up to 720 days can occur, but the literature demonstrated that eggs are still viable up to 492 days. In some studies, the highest hatching rate (97.2%) occurs after 121 days quiescence [59, 60]. In another study, high hatching occurs after 180 days [23]. Among these quiescence periods, the 121 days period is the most favorable to *Ae. aegypti*, with significantly higher hatching rate and number of cycles (groups) than for other periods.

Other authors [32, 34, 36] also observed the same phenomenon attributing to different factors these prolonged periods of viability that include resistant, durable, inactive and residual eggs. Whatever the factor is, quiescence provoked by climatic variables, such as the decrease of humidity and temperature, increases *Ae. aegypti* life expectancy by enabling re-growth of the species. This behavior is relevant to the control of this mosquito, since the eggs adhered to container walls resist desiccation and can hatch when the water level rises.

In dechlorinated water at 26°C, there is a 92% *Ae. aegypti* larvae survival rate [60]. The *Ae. aegypti* larvae grown in raw sewage water show shorter developmental periods, probably due to the high concentrations of organic materials that serve as nutrients, although the authors hypothesized that the surface tension and high viscosity of the water are responsible. Further, the formation of material on the surface may makes it difficult for the larvae to obtain atmospheric oxygen. Beserra et al. [60] showed that *Ae. aegypti* can develop in polluted environments such as domestic sewage, where there is a high concentration of organic material and practically zero DO (0.12 mg L^{-1}), as well as in treated effluents, with carbonaceous material removed, as the post-treated effluent after anaerobic filter and in a polishing pond.

Notably, food availability is a decisive condition in the selection of the breeding site by the female, even in conditions considered unfavorable with regards to the available water quality, including high pollution levels. Beserra et al. [60] analyzed water quality and food availability for *Ae. aegypti* larvae. Water quality elongates the breeding period, with or without food and the medium turbidity decreases. Further, turbidity is an important parameter and low light penetrability in the aquatic environment is beneficial for the species, since *Ae. aegypti* larvae are photophobic. The *Ae. aegypti* is a competent vector for the transmission of flavivirus, which causes yellow fever and dengue fever. In this organism, there are at least 10 different rhodopsins. Mosquitoes have similar sets of rhodopsin and retinal organization, including the malaria vector *Anopheles gambiae* (Giles) (Diptera: Culicidae) that diverged from *Ae. aegypti* millions of years ago. Conservation of molecules within these visual systems implies that these species have visual processing capabilities similar to those of the common ancestor. Thus, these capabilities remain important for the suitability of existing species and their adaptability to environmental conditions. In *Ae. aegypti*, several mechanisms contribute to the ability of a photoreceptor to adapt to ambient light conditions. The *Ae. aegypti* expresses long wavelength rhodopsin Aaop1 on all R1–6 photoreceptors and most R8 photoreceptors. These photoreceptors alter the cellular location of Aaop1 and rearrange their photosensitive rabdomeric membranes daily [61].

The effects of temperature on *Ae. aegypti* larval behavior have been examined for different food availability conditions at breeding sites. With reduced food availability and low temperature, the larvae spend more time and energy to feed. At the temperature extremes, there are negative impacts on feeding behavior and larval activity [62].

Increasing viscosity by elevating the concentration of dissolved solids imposes unfavorable conditions, including limiting movement of the organisms. However, females adapt, choosing to perform oviposition even under unfavorable conditions. This phenomenon shows that for *Ae. aegypti*, the water physicochemical quality is not the most important parameter, but rather the conditions that the breeding site presents for the development and survival of the immature individuals are crucial.

Albeny-Simões et al. [63] showed that the choice of breeding grounds for oviposition and reproduction with aquatic larvae is influenced by the risk of offspring mortality and survival, and food availability. Studies revealed that *Ae. aegypti* is attracted to do the oviposition in breeding sites with predatory larvae (*Toxorhynchites* (Theobald) (Diptera: Culicidae)), as the density of dead larvae and metabolic products increase the bacterial abundance in the breeding location. Bacterial biomass and species composition are environmental determinants for the occurrence and abundance of *Aedes* spp., breeding sites with competing species [64, 65].

Soares Pinheiro et al. [66] evaluated *Ae. aegypti* viability in the Amazon region that has high humidity. The *Ae. aegypti* eggs have been stored in plastic cups, paper envelopes or plastic bags and maintained in internal and external areas for different times. Overall, the storage form is important for egg viability. The authors concluded that *Ae. aegypti* viability in the Amazon region is maintained at high levels up to 4 months, at which time there are drastic reductions and hatchings up to 8 months occur at very low percentages. These results show that excess humidity and temperature can induce constant stimuli to hatching eggs and possibly due to water stress, reduce their viability. Comparatively, in dry environments this viability can be preserved for up to 492 days [59]. In this regard, the selection of suitable place for oviposition is fundamental for the distribution and establishment of *Ae. aegypti*. Studies indicate that *Ae. aegypti* females are not attracted to breeding grounds with clean water. This flexibility to choose breeding sites for posture, despite the apparent risks to reproduction, is an important fact. This posture behavior demonstrates the adaptability of the insect to the different environmental situations, even though they appear to represent unfavorable conditions [61, 62].

Additionally, breeding sites of principal dengue virus spreader *Ae. aegypti* [67] and secondary vector *Ae. albopictus* [68] or both [69] can be stopped through biological control [70]; with environmental modifications [71]; utilizing copepods (H. Milne-Edwards) (Copepoda: Cyclopidae) [72]; and using ecological services by frogs, toads and tadpoles (Anura) [73].

3. Conclusions

Studies aimed the understanding of the life cycle and development of Culicidae mosquitoes and their association with breeding sites are extremely important, since the main control actions are performed in these microhabitats. Although many researchers have devoted themselves to this topic, elucidating the main factors associated with the development of immature forms and seeking new control alternatives, what we have observed is that these insects can colonize new microhabitats, expanding to new areas and reaching high levels of infestation, resulting in outbreaks and epidemics of some arboviruses, such as dengue, chikungunya and zika.

The main factor contributing to this fact is the high adaptive power that these insects have in colonizing new breeding sites, the natural ones, but especially the artificial ones, located in urban environments, which are increasingly available due to the lack of investment in the improvement of sanitary conditions in cities, disorderly expansion of urban centers, increase of consumable products in disposable packaging, among others.

The available studies on the type, frequency and colonization of *Aedes* spp. breeding sites show that artificial breeding sites are preferred, and can be colonized by *Aedes* and other associated species. Natural breeding sites in plants, rocks and organic remains can be colonized for long periods, preferably by *Ae. albopictus* and occasionally by *Ae. aegypti*. These preferences can be reversed based on climatic influences, food availability, and the breeding water physicochemical and biological conditions. The breeding sites most suitable for *Aedes* spp. reproduction have a considerable amount of decomposing organic matter and conditions that guarantee a reproductive advantage to these species.

Mosquito population control is dependent on adherence and awareness of populations and knowledge of breeding conditions. Population control interventions with new products with potentially wide use or efficient strategies that are based on habits and ecological knowledge of breeding sites can be advantageous for *Ae. aegypti* population and reproduction control.

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