# Chapter 4. Ecology of the mosquito Ae. aegypti

This chapter considers the ecology of Aedes aegypti. Elements are provided on niche modelling and the species distribution modelling. The limited trophic interactions of this mosquito and its development in anthropic habitats and urban environments are detailed, followed with considerations on its abiotic requirements and tolerance in aquatic and terrestrial conditions. Information is also provided on the Ae. Aegypti biotic interactions in the landscape, its life history traits and fitness influencing dispersal patterns and population density and distribution. Elements are given on population models being developed (spatial-temporal dynamics).

## Ecological niche/species distribution modelling of Ae. aegypti

The ecological niche of a species can be defined as the range of environmental and biotic conditions within which its populations can persist without immigration (Hutchinson, 1957). The range of environmental and biotic conditions can be assessed through niche modelling, providing evidence for geographic isolation between populations (either based on conserved or divergent ecological niches). By mapping the spatial distribution of environmental suitability of climatic variables (Raxworthy et al., 2007), the niche modelling provides a much stronger case for geographic isolation for populations isolated by intervening unsuitable regions reducing gene flow.

The population structure of *Ae. aegypti* is complex, varies by region and scale, and can be influenced by environment and geography (Yan, Chadee and Severson, 1998; Urdaneta-Marquez et al., 2008). Urban estimates of genetic differentiation have varied in part due to environmental conditions and dispersal patterns (Huber et al., 2002; da Costa-Ribeiro, Lourenço-de-Oliveira and Failloux, 2006). *Ae. aegypti* population dynamics in urban areas are subject to daily as well as seasonal meteorological variability (Halstead, 2008). Effects of seasonal climatic factors on mosquito life-history traits are well documented, particularly on adult distribution, survival and availability of oviposition sites. Several supportive studies have also been made on physiologic aspects such as decreased embryonic (e.g. Trpis, Haufe and Shemanchuk, 1973) and larval (e.g. Teng and Apperson, 2000) development times as well as decreased size of adults (e.g. Rueda et al., 1990) being associated with higher temperature.

It may be an oversimplified assumption that climate change will independently lead to an increased range for this species and a concomitant expansion of the risk of dengue infections around the world. A range of dynamic factors must be considered when predicting future global distribution trends. Constraining the focus of models to a local and/or regional scale rather than aspiring for global models may increase their predictive capacity. In light of climate change, the major drivers of future dengue susceptible areas will likely include unprecedented population growth, particularly in urban areas in the tropics; an increase in the movement of both vector and virus reservoirs via modern transport; and a lack of effective mosquito management (Mackenzie, Gubler and Petersen, 2004). More details are given in the "Abiotic requirements and tolerance" section below.

#### Ae. aegypti niche and trophic interactions

The mosquito *Ae. aegypti* has a relatively narrow niche with limited trophic interactions. The anthropophilic form of *Ae. aegypti, Ae. aegypti aegypti,* utilises flooded artificial containers as habitat for larvae and pupae. It is this form that has become established in most tropical and subtropical areas globally and is the primary vector of dengue, Zika and several other viruses. The original sylvan form of *Ae. aegypti, Ae. aegypti, formosus,* occurs in sub-Saharan Africa where natural containers such as flooded tree holes are the dominant larval habitat (Lounibos, 1981). A plethora of man-made objects composed of plastic, rubber, metal, concrete, masonry and ceramics have been shown to hold water, capture nutrients and produce *Ae. aegypti* (Ritchie, 2014). Within these flooded containers, larvae graze on the surface of the container, feeding on fallen detritus (typically leaves) and bacteria and algae that have grown on it. Protein sources such as insects, seeds, fruit and even dead conspecific mosquito larvae are fed upon. However, many of these containers are nutrient poor, especially covered containers such as water storage tanks, and typically produce stunted adults. The restriction of nutrients, coupled

with high larval populations beyond the carrying capacity of the container, reduce larval growth and pupation via density-dependent regulation (Hancock et al., 2016). Indeed, it is the sudden input of protein from, for example, a cricket that falls into and drowns within the container, which can lead to a surge in larval growth, pupation and adult emergence.

There is a very limited number of species known to feed upon *Ae. aegypti* larvae and pupae. Most artificial containers are small to medium in size, only intermittently flooded and thus do not maintain populations of predaceous aquatic insects or vertebrates such as fish and amphibians. While many of these aquatic predators can eat mosquito larvae, they are uncommon in most *Ae. aegypti* habitat. In some larger containers, dytiscid beetles and dragonfly naiads can occur and feed upon mosquito larvae, while fish and tadpoles have been propagated and released in large water storage containers to control *Ae. Aegypti*. Among the many kinds of mosquito that do not consume blood, mosquitoes of the genus *Toxorhynchites* oviposit in artificial containers and selectively feed upon mosquito larvae (Trpis, 1973) being *Ae. aegypti* larvae as well as from other container mosquito species such as *Ae. albopictus* and *Ae. notoscriptus*. Copepods of the genus *Mesocyclops* will actively predate first instar larvae of *Ae. aegypti*.

Adult Ae. aegypti are also restricted to largely "artificial habitats" created by man. This "cockroach of mosquitoes", as it is often called, prefers to harbour inside buildings and houses in urban areas where it has ready access to humans for blood feeding. In some instances, all life stages of Ae. aegypti (egg, larvae, pupae and adult) can occur inside, especially in areas where water is stored indoors for domestic use. However, in many areas Ae. aegypti adults do spend considerable time outdoors where they seek flooded containers in which to oviposit. Predation of adult Ae. aegypti is poorly studied. Spiders, especially saltidae (jumping spiders), are known to actively stalk and feed upon adult mosquitoes indoors (Sulaiman et al., 1990) and can be a major predator in semi-field cages (S. Ritchie personal observation). Most other animals purportedly linked to adult mosquito predation, such as bats, geckoes and dragonflies, often feed either crepuscularly or at night, and would likely miss day active Ae. aegypti. Ants and cockroaches are known to feed upon Ae. aegypti eggs in containers (see below the section on "Biotic interactions in the landscape"), and mites and booklice often predate eggs in laboratory colonies and thus potentially would in the field. Ants readily consume dead adult mosquitoes on the ground and even stranded larvae in recently dried containers. As Ae. aegypti occurs in relatively low numbers (generally < 10 adults per house), the biomass of this mosquito is small (an estimated 2 g/ha in Cairns, Queensland, Australia [S. Ritchie, unpublished data]) and it is usually considered that it does not make a large trophic contribution.

In summary, urbanised *Ae. aegypti (Ae. aegypti aegypti)* is largely restricted to artificial, man-made habitats in geographic areas outside of its native range. Endemic species within "natural" tropical ecosystems are not trophically connected with *Ae. aegypti aegypti*, or in a limited way. Thus, it is assumed that they are at minimal risk should the species be eliminated from those areas.

# **Anthropic habitats**

Increase in the size and population density of major cities place increasing demands on infrastructure and essential services, particularly in developing countries. The response to these demands may dramatically alter the suitability of a locality for urban mosquito breeding. An absence or irregularity of water supply will lead to an increase in domestic water storage practices which, in turn, will alter the landscape of potential *Ae. aegypti* habitat, perhaps providing a far more regular or abundant supply of larval sites.

The effects of topographic features of urban environments on *Ae. aegypti* behaviour are not fully understood; however, Reiter et al. (1995) noted that buildings were not an impediment to *Ae. aegypti* flight. Certain results indicate that urban landscape does contain barriers to dispersal (Reiter et al., 1995; Chadee, 2004; Valerio et al., 2012), and this affects the mosquito population structure.

Such information can be useful to agencies in charge of vector control for better targeting mosquito populations and areas of higher risk within control zones. Understanding the role of landscape features on population dispersal is likely critical to achieving success with any *Ae. aegypti* control strategy (more information is given in Annex A. Control of the mosquito *Ae. aegypti*).

#### **Abiotic requirements and tolerance**

Considerable variation in adult size occurs as a result of habitat conditions such as water quality, food availability, and crowding during mosquito larval breeding (Nasci, 1991). The adult size strongly influences various aspects of mosquito life history: survivorship (Pumpuni and Walker, 1989), mating success (Yuval, Wekesa and Washino, 1993), blood meal size (Xue, Edman and Scott, 1995), parous rate (Haramis, 1983), fecundity (Packer and Corbet, 1989), dispersal (Renshaw, Service and Birley, 1994) and longevity (Feinson and Spielman, 1980). Among abiotic and biotic factors, high temperature and low nutrition in the developing stages of mosquitoes generally result in small adults. While temperature, humidity and rainfall have overt impacts on mosquito adult survival and ecology, other climatic factors such as photoperiod and wind velocity may also be influential. Importantly, it is necessary to consider that these meteorological conditions have a combined effect on the survival and development of mosquitoes and that it is difficult to examine the potential impact of these factors independently as a consequence (Jansen and Beebe, 2010).

#### Aquatic

*Ae. aegypti* prefers clean water found in many types of domestic containers inside or near human dwellings (Nazri et al., 2013). The *Aedes* mosquito larvae require standing water to complete their growth cycle, therefore, any body of standing water represents a potential *Aedes* mosquito breeding site for mosquito larvae to mature. Water quality affects the productivity of a potential mosquito breeding habitat. Typically, greater numbers of mosquitoes are produced in water bodies with poor circulation, higher temperatures and higher organic content than in water bodies having good circulation, lower temperatures and lower organic content (Focks et al., 1993; Murrell and Steven, 2008).

Aquatic habitats for *Ae. aegypti* are containers in which eggs develop into adult mosquitoes. Mosquitoes lay eggs on the walls of water-filled containers in or around the house. The eggs hatch when submerged in water and can survive desiccation for months (see section on Morphology in Chapter 1). There is a great variety of man-made containers on backyards or patios that collect rainwater or that are filled with water by people. Artificial or natural water containers (water storage containers, flower pots, discarded tires, plates under potted plants, cemetery vases, flower pots, buckets, tin cans, clogged rain gutters, ornamental fountains, drums, water bowls for pets, birdbaths, etc.)

that are within or close to places where humans live are ideal larval habitats for this mosquito.

#### **Terrestrial**

Studies of associations between climate parameters and *Ae. aegypti* are complicated by the dependence of the mosquito on humans, especially its preference for human blood and its adaptation to use artificial containers as larval development sites (Focks and Alexander, 2006; Tun-Lin et al., 2009).

*Ae. aegypti* is the major urban vector of DENV worldwide. Over the last 25 years, there has been a global increase in both the distribution of *Ae. aegypti* and epidemic DENV activity (Mackenzie, Gubler and Petersen, 2004). Historically, *Ae. aegypti* has been thought to be able to establish in regions between the northern January and southern July 10°C isotherms, while more recent studies suggest that the 15°C yearly isotherm is a better estimate (see Chapter 1 section on "Origin and current geographic distribution").

Although *Ae. aegypti* is generally considered a tropical mosquito (Christophers, 1960), it should be noted that its distribution in some temperate regions of the world does appear to be influenced by climate variables (Liu-Helmersson et al., 2016).

The potential effects of climate and environmental change on Ae. aegypti and DENV transmission have generated much debate (Jetten and Focks, 1997; Patz et al., 1998; Hales et al., 2002; Barclay, 2008; Beebe et al., 2009; Ooi and Gubler et al., 2009; Banu et al., 2011; Brady et al., 2013, 2014). Part of this controversy relates to modelling future climate-driven change for the vector or disease without accounting for human-related factors, which also impact the vector itself (e.g. availability of water-filled artificial containers as larval development sites) or DENV transmission dynamics (e.g. serotypespecific susceptibility of the human population). Several reports consider that the domestic nature of this species probably exerts more influence on its distribution than climate variables. These confounding factors can, thus, modulate the effects of climate change on the mosquito distribution. It is also recognised that the effects of climate and environmental change are location-specific and likely to impact Ae. aegypti and, potentially, also DENV transmission to a greater extent in some geographic areas than others (Lozano-Fuentes et al., 2012). Studies in Australia suggest that future changes in Ae. aegypti distribution in the country may not be directly caused by climate change but rather, by human response to changing rainfall patterns by increased or decreased use of water storage containers (Beebe et al., 2009; Russell et al., 2009; Williams et al., 2010, 2014, 2015; Bannister-Tyrrell et al., 2013).

#### **Biotic interactions in the landscape**

Biological interactions between species occupying similar niches may also influence the distribution and abundance of *Ae. aegypti*. Whilst a number of underlying processes including interspecific larval resource competition has been suggested (Lounibos et al., 2002; Juliano and Lounibos, 2005), it is most likely that multiple factors determine the current distributions of each species. Examples of these interconnected factors include the potentially asymmetrical effects of abiotic factors (including climate) on different life cycle stages as underlined above, apparent competition induced by parasites, mating interference and variation between the microclimates in given locations (Lounibos et al., 2002; Juliano and Lounibos, 2005).

In the aquatic environment, the larvae have a number of predators including other invertebrates, tadpoles and fish. Aquatic invertebrate predators from the Coleoptera (beetles), Diptera (flies including the predaceous mosquito *Toxorhynchites* spp.), Hemiptera (true bugs) and Odonata (dragonflies and damselflies) orders prey on all mosquito larvae in the same environment (Shaalan and Canyon, 2009). Because *Ae. aegypti* usually uses man-made containers as breeding sites, it does not seem to have specific predators but rather "opportunistic" ones that feed on larvae if encountering them, as detailed under a previous section dealing with trophic interactions. Predators can significantly affect the survival, development, and recruitment levels of mosquitoes in their aquatic breeding sites. There is also some evidence that the occasional presence of predators in vessels can favour oviposition by *Ae. aegypti*, the mosquitoes being attracted to predator kairomones<sup>1</sup> (Albeny-Simões et al., 2014). Mogi (2007), however, reviewed mosquito invertebrate predators and concluded that they are usually absent or sparse in man-made containers in residential areas.

Russell, Kay and Shipton (2001) placed filter-paper strips containing *Ae. aegypti* eggs within flooded telecommunication pits and surface containers in Charters Towers (Australia), and found that no subterranean eggs and only 1% of surface-placed eggs, respectively, survived the 4-month dry season despite the egg capacity to survive desiccation for months (see Chapter 2, section on Life cycle). In this case, predation was primarily by cockroaches. Attack by a fungus (*Penicillium citrinum*) also resulted in high mortality within the flooded subterranean site. The high mortality of eggs in subterranean sites led the authors to conclude that subterranean egg refugia were not responsible for the reintroduction of *Ae. aegypti* into surface containers at the onset of the wet season.

Ants are also a significant predator of *Ae. aegypti* eggs in colonies, and probably also in the field (Focks et al., 1993; Russell, Kay and Shipton, 2001; Ritchie, 2014).

#### Life history traits and fitness

The body size of mosquitoes can influence a number of bionomic factors, such as their blood-feeding ability, host attack rate and fecundity (Klowden and Lea, 1978; Xue, Edman and Scott, 1995; Farjana and Tuno, 2012). All of these traits are important determinants of their potential to transmit diseases (Farjana and Tuno, 2013).

*Ae. aegypti*, the container-breeding mosquito, is closely associated with humans and highly anthropophilic, tending to predominate in densely populated urban areas. They are commonly found indoors, breeding in artificial containers, with female needing to feed on blood to produce eggs, as described above. Studies have demonstrated high anthropophily, with over 90% of the ingested blood being human, and the rest from pets, such as dogs and cats (Scott et al., 1993). Multiple feeding in a gonotrophic cycle can increase the risk of disease transmission by increasing the frequency of contact with hosts (Garrett-Jones, 1964; Garrett-Jones and Shidrawi, 1969; Dye, 1986). Two types of multiple feeding have been recognised: supplementary feeding owing to nutritional reserve depletion in teneral females (Scott et al., 1993; Xue, Edman and Scott, 1995; Scott et al., 2000; Reyes-Villanueva, 2004) and interrupted feeding owing mainly to host defence (Clements, 1999). For more detailed information, see Chapter 2 section on "Physiology of reproduction".

## Dispersal

Landscape fragmentation and human demography can influence dispersal patterns of mosquitoes. The degree and nature of modification can affect the flow of genes

conditioning vector competence and insecticide resistance (Hemme et al., 2010). Generally anthropic habitats minimise climatic variation where *Ae. aegypti* distribution is dependent on human behaviour (Jansen and Beebe, 2010).

Mosquito dispersal patterns are non-random and influenced by environmental factors as reported by Sheppard et al. (1969) and Hausermann, Fay and Hacker (1971) in *Ae. aegypti* mosquitoes using mark-release-recapture method. Ecological features including accessible water, vegetation patterns, humidity, contribute to determining the mosquito distribution. The range of dispersal is dependent upon a mosquito's ability to remain in flight and the availability and abundance of shelter, food sources, hosts for blood meals and suitable oviposition sites (Sheppard et al., 1969). Suitable host availability may reduce dispersal as reported by Suwonkerd et al. (2006) where fewer *Ae. aegypti* mosquitoes exited a hut when a human host was present compared to controls with the presence a dog, or with no human host.

Given that dispersal range is an important aspect of dengue transmission, much research has been conducted attempting to determine how far *Ae. aegypti* adults travel. A characteristic feature of *Ae. aegypti* is that they rarely disperse far from where they eclose (i.e. emergence as an adult from the pupa) (Getis et al., 2003), therefore, the presence of adult forms is for practical purposes an accurate indication of the proximity of breeding sites. Adults only disperse further when a vital requirement is limiting or absent or there is a disturbance. Typically, adult *Ae. aegypti* mosquitoes travel relatively short distances of up to 100 m, although longer dispersal estimates of about 800 m have been observed, particularly when host density is low and female mosquitoes are starved (McDonald, 1977; Honório et al., 2003; Harrington et al., 2005).

Overall, most studies show a very short dispersal distance for *Ae. aegypti*. This species has been reported to usually fly from 50 m to 300 m during its lifetime, with mean dispersal distances of 28 m to 199 m (Harrington et al., 2005). Experiments in different parts of the world involving the release and recapture of adults suggest that most are recovered within 20 m to 50 m of the release point, with a small percentage reaching distances greater than 170 m and not more than 200 m (Morlan and Hayes, 1958; Sheppard et al., 1969; McDonald, 1977; Trpis and Häusermann, 1986; Rodhain and Rosen, 1997; Muir and Kay, 1998; Ordoñez-Gonzalez et al., 2001; Harrington et al., 2005; Russell et al., 2005; Maciel-de-Freitas, Codeço and Lourenço-de-Oliveira, 2007a, 2007b; Valerio et al., 2012).

Even if important variations in mosquito daily and lifetime dispersal rates have been reported, however, the examination of the mean distance travelled (MDT) and the flight range of mosquitoes, as opposed to the maximum distance travelled, may be a more epidemiologically-important parameter (Harrington et al., 2005). Many studies using mark-release-recapture methods (above-mentioned) have reported a flight range for *Ae. aegypti* shorter than the largest observed dispersal of 800 m. And the majority of re-captured mosquitoes were collected at the house of release or neighbouring houses, suggesting females are rarely expected to visit more than two or three houses in their lifetime. In a Kenyan village, McDonald (1977) recaptured a majority of mosquitoes within the house where they were released over 12 days. Marked mosquitoes released in a tire dump in New Delhi, India, dispersed with maximum distances from 50 m to 200 m, but most were recaptured within 50 m of the release point (Reuben, Yasuno and Panicker, 1972). Similarly, Muir and Kay (1998) reported females having a MDT of 56 m.

It has also been observed that females are less likely to disperse from houses with a large number of available oviposition sites (Edman et al., 1998). Given that most *Ae. aegypti* 

do not disperse very far, containers in close proximity to other productive vessels are more likely to be oviposition sites and to receive a large number of eggs. Holding other attributes constant, containers in areas of dense larval habitat will have a greater probability of being productive with a greater abundance of pupae than areas where suitable wet containers are rare and thus have a spatially-dispersed distribution. This low dispersal is a limit to the use of the autodissemination technique<sup>2</sup> for control in large areas, which would require a high density of dissemination stations (Devine et al., 2009).

In some studies, released mosquitoes tended to cluster around houses with some dispersal towards adjacent houses, and mosquitoes released on the perimeter of villages moved towards the centre of the village (Sheppard et al., 1969; Trpis and Hausemann, 1986; Getis et al., 2003; Harrington et al., 2005; Maciel-de-Freitas et al., 2006). The relatively large numbers and duration of DENV infected females captured in houses with confirmed dengue cases in Merida, Mexico may further indicate high fidelity between *Ae. aegypti* mosquitoes and place of pupal emergence (García Rejón et al., 2008).

The rate at which *Ae. aegypti* spreads to new areas outside of its native range is highly correlated with human activities that aid in its dispersal, including modes of transport. Boats, planes and terrestrial vehicles (e.g. cars, trucks, buses) also play a role on long-range human-mediated dispersal of adults and eggs. *Ae. aegypti* can "hitch a ride" in these vehicles, resulting in long-distance transport (Ritchie, 2014). In the Peruvian Amazon the incidence of *Ae. aegypti* coincides with interconnecting roads and highways and to a lesser extent, routes of boat traffic between ports (Guagliardo et al., 2014). Abandoned bottles, tires and other containers resulting from human activities along these travel routes provide a favoured habitat for the larval development of *Ae. aegypti* (Flores et al., 2005) and likely play a role in expanding its range. Furthermore, Chadee, Doon and Severson (2007) indicated that prevailing weather patterns may potentially influence dispersion.

Results from two classes of markers (SNPs) show strong evidence of limited gene flow across Uriah Butler Highway (UBH) in Trinidad island (Trinidad and Tobago), effectively fragmenting the populations on the east and west side of the highway (Hemme et al., 2010). Although the distance across the highway is well within dispersal estimates for *Ae. aegypti*, lack of cover and shade may have made the UBH a harsh environment for mosquitoes to transect. This is supported by Tun-Lin, Kay and Barnes (1995) who reported shade as a significant factor impacting the presence of *Ae. aegypti* in premise surveys and Russell et al. (2005) confirmed that released *Ae. aegypti* dispersal patterns were non-random with more mosquitoes being recaptured along a corridor with heavy shading from trees and vegetation. Furthermore, oviposition sites were most likely minimal, even along peripheral ditches and absence of blood meal hosts may have dissuaded migration across the UBH and prevented a stepping stone model of colonisation from occurring over UBH.

#### Population density and distribution

A primary determinant of adult mosquito population density concerns the types and number of containers in a given environment. Adult production is unevenly distributed across potential larval development sites.

In most cases, a few key types of containers are responsible for a large proportion of the pupal, and thus adult, production (Morrison et al., 2004; Focks and Alexander, 2006; Koenraadt et al., 2008). Protective measures such as lids, larvicide, removal of discarded and unused containers or biological agents have reduced adult vector population density

(Kay and Nam, 2005; Morrison et al., 2008). Container capacity, water temperature, source of water and container location, all of which can vary seasonally (Strickman and Kittayapong, 2002; Lenhart et al., 2006; Koenraadt et al., 2008), have been cited as important ecological factors affecting the production of adult *Ae. aegypti* (Morrison et al., 2004; Barrera, Amador and Clark, 2006a). Access to humans for blood feeding is additionally important for the production of *Ae. aegypti* adults (Ritchie, 2014).

A number of studies have also found that *Ae. aegypti* abundance is not homogeneous among households, with disproportionate numbers of immature and adult mosquitoes clustered in key premises (Tun-Lin, Kay and Barnes, 1995; Getis et al., 2003; Barrera, Amador and Clark, 2006b). A study of *Ae. aegypti* production in American Samoa found that containers were more productive on average in houses with a large number of containers (Lambdin et al., 2009). To this point, the relationship between productivity and the spatial distribution of containers has not been rigorously examined.

#### **Population modelling**

Spatial models of *Ae. aegypti* could provide an important advance toward model-guided vector control and risk assessment (Williams et al., 2008; Xu et al., 2010). One of the key challenges in modelling *Ae. aegypti* is the lack of adequate data for validation. Most models seek to represent the temporal dynamic response to climate and endogenous forces (Focks et al., 1993; Ferreira and Yang, 2003; Otero, Solari and Schweigmann, 2006; Williams et al., 2013), while others consider the spatial-temporal dynamic by introducing dispersal mechanisms (Otero, Schweigmann and Solari, 2008; Magori et al., 2009; Almeida et al., 2010).

Models describing the population dynamics of *Ae. aegypti* are either deterministic (Ferreira and Yang, 2003) or stochastic (Otero, Solari and Schweigmann, 2006) and share a common structure based on the framework of System Theory (Bertalanffy, 1975). Few available computational models simulate *Ae. aegypti* spatial-temporal dynamics. Otero, Schweigmann and Solari (2008) proposed a stochastic spatially-explicit model, based on their previous temporal model (Otero, Solari and Schweigmann, 2006), in which space is modelled as cells which are occupied by autonomous mosquito populations interconnected by flying individuals. Dispersal between cells is modulated by the availability of breeding sites. A similar approach considered both the spatial distribution of breeding sites and the dynamics of the aquatic stage of the mosquitoes (larvae and pupae) (Focks et al., 1993; Magori et al., 2009).

#### Notes

<sup>&</sup>lt;sup>1</sup> Kairomones are semiochemicals similar to pheromones but differing by the fact that they send signals between different species.

<sup>&</sup>lt;sup>2</sup> See more information on this technique in Annex A. Section: Chemical control.

#### References

- Albeny-Simões, D. et al. (2014), "Attracted to the enemy: Aedes aegypti prefers oviposition sites with predatorkilled conspecifics", Oecologia, Vol. 175, pp. 481–492.
- Almeida, J.S. et al. (2010), "Multi-agent modelling and simulation of an Aedes aegypti mosquito population", Environmental Modelling and Software, Vol. 25, No. 12, pp. 1490-1507.
- Bannister-Tyrrell, M. et al. (2013), "Weather-driven variation in dengue activity in Australia examined using a process-based modelling approach", *American Journal of Tropical Medicine and Hygiene*, Vol. 88, No. 1, pp. 65-72.
- Banu, S. et al. (2011), "Dengue transmission in the Asia-Pacific region: Impact of climate change and socioenvironmental factors", *Tropical Medicine & International Health.*, Vol. 16, pp. 598-607.
- Barclay, E. (2008), "Is climate change affecting dengue in the Americas?", *Lancet*, Vol. 371, No. 9617, pp. 973-974.
- Barrera, R., M. Amador and G.G. Clark (2006a), "Ecological factors influencing *Aedes aegypti* (Diptera: Culicidae) productivity in artificial containers in Salinas, Puerto Rico", *Journal of Medical Entomology*, Vol. 43, pp. 484-492.
- Barrera, R., M. Amador and G.G. Clark (2006b), "Use of the pupal survey technique for measuring Aedes aegypti (Diptera: Culicidae) productivity in Puerto Rico", *The American Journal of Tropical Medicine and Hygiene.*, Vol. 74, pp. 290-302.
- Beebe, N.W. et al. (2009), "Australia's dengue risk driven by human adaptation to climate change", *PLoS Neglected Tropical Diseases*, Vol. 3: e429.
- Bertalanffy, L.V. (1975), Perspectives on General Systems Theory. Scientific-Philosophical Studies, E. Taschdjian (eds.), New York: George Braziller, ISBN 0-8076-0797-5 (in Portuguese), Vozes.
- Brady, O.J. et al. (2014), "Global temperature constraints on *Aedes aegypti* and *Ae. albopictus* persistence and competence for dengue virus transmission", *Parasites and Vectors*, Vol. 7, pp. 338.
- Brady, O.J. et al. (2013), "Modelling adult *Aedes aegypti* and *Aedes albopictus* survival at different temperatures in laboratory and field settings", *Parasit Vectors*, Vol. 6, pp. 351.
- Chadee, D.D. (2004), "Observations on the seasonal prevalence and vertical distribution patterns of oviposition by Aedes aegypti (L.) (Diptera: Culicidae) in urban high-rise apartments in Trinidad, West Indies", Journal of Vector Ecology, Vol. 29, No. 2, pp. 323-330.
- Chadee, D.D., R. Doon and D.W. Severson (2007), "Surveillance of dengue fever cases using a novel Aedes aegypti population sampling method in Trinidad, West Indies: the cardinal points approach", Acta Tropica, Vol. 104, pp. 1-7.
- Clements, A.N. (1999), The Biology of Mosquitoes, Volume II. "Sensory Reception and Behaviour", CABI Publishing, Oxon.
- Da Costa-Ribeiro, M.C.V., R. Lourenço-de-Oliveira and A.B. Failloux (2006), "Geographic and temporal genetic patterns of *Aedes aegypti* populations in Rio de Janeiro, Brazil", *Tropical Medicine & International Health*, Vol. 11, pp. 1276-1285.
- Devine, G.J. et al. (2009), "Using adult mosquitoes to transfer insecticides to Aedes aegypti larval habitats", Proceedings of the National Academy of Sciences of the United States of America, Vol. 106, pp. 11530-11534.
- Dye, C. (1986), "Vectorial capacity: Must we measure all its components?", Parasitology, Vol. 2, pp. 203-209.
- Edman, J. et al. (1997), "Attractant resting boxes for rapid collection and surveillance of *Aedes aegypti* (L.) inside houses", *Journal of the American Mosquito Control Association*, Vol. 13, pp. 24-27.
- Farjana, T. and N. Tuno (2013), "Multiple blood feeding and host-seeking behavior in *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae)", *Journal of Medical Entomology*, Vol. 50, No. 4, pp. 838-846.
- Farjana, T. and N. Tuno (2012), "Effect of body size on multiple blood feeding and egg retention of *Aedes aegypti* (L.) and *Aedes albopictus* (Skuse) (Diptera: Culicidae)", *Medical Entomology and Zoology*, Vol. 63, pp. 1-9.

- Ferreira, C. and H. Yang (2003), "Study population dynamics of Aedes aegypti mosquito (in Portuguese)", Tendências em Matemática Aplicada e Computacional [Trends in Applied and Computational Mathematics], Vol. 4, No. 2, pp. 187-196.
- Flores, A.E. et al. (2005), "Elevated alfa-esterases levels associated with permethrin tolerance in *Aedes aegypti* (L.) from Baja California, Mexico", *Pesticide Biochemistry and Physiology*, Vol. 82, pp. 66-78.
- Focks, D.A. and N. Alexander (2006), A Multi-Country Study on the Methodology for Surveys of Aedes aegypti Pupal Productivity: Findings and Recommendations, World Health Organization, Geneva.
- Focks, D.A. et al. (1993), "Dynamic life table model for *Aedes aegypti* (Diptera: Culicidae): Simulation results and validation", *Journal of Medical Entomology*, Vol. 30, pp. 1003-1028.
- García-Rejón, J.E. et al. (2008), "Dengue virus-infected Aedes aegypti in the home environment", American Journal of Tropical Medicine and Hygiene, Vol. 79, No. 6, pp. 940-950.
- Garrett-Jones, C. (1964), "Prognosis for interruption of malaria transmission through assessment of the mosquito's vectorial capacity", *Nature*, Vol. 204, pp. 1173-1175.
- Garrett-Jones, C. and G.R. Shidrawi (1969), "Malaria vectorial capacity of a population of Anopheles gambiae", Bulletin of the World Health Organization, Vol. 40, pp. 531-545.
- Getis, A. et al. (2003), "Characteristics of the spatial pattern of the dengue vector, *Aedes aegypti*, in Iquitos, Peru", *The American Journal of Tropical Medicine and Hygiene*, Vol. 69, pp. 494-505.
- Guagliardo, S.A. et al. (2014), "Patterns of geographic expansion of *Aedes aegypti* in the Peruvian Amazon", *PLoS Neglected Tropical Diseases*, Vol. 8, No. 8: e3033.
- Hales, S. et al. (2002), "Potential effect of population and climate changes on global distribution of dengue fever: An empirical model", *Lancet*, Vol. 360, pp. 830-834.
- Halstead, S.B. (2008), "Dengue virus Mosquito interactions", Annual Review of Entomology, Vol. 53, pp. 273-291.
- Hancock, P.A. et al. (2016), "Density dependent population dynamics in *Aedes aegypti* slow the spread of wMel *Wolbachia*", *Journal of Applied Ecology*, Vol. 53, No. 3, pp. 785-793.
- Haramis, L.D. (1983), "Increased adult size correlated with parity in *Aedes triseriatus*", *Mosquito News*, No. 43, pp. 77-79.
- Harrington, L.C. et al. (2005), "Dispersal of the dengue vector Aedes aegypti within and between rural communities", American Journal of Tropical Medicine and Hygiene, Vol. 72, No. 2, pp. 209-220.
- Hausermann, W., R.W. Fay and C.S. Hacker (1971), "Dispersal of genetically marked female Aedes aegypti in Mississippi", Mosquito News, Vol. 31, pp. 37-51.
- Hemme, R.R. et al. (2010), "Influence of urban landscapes on population dynamics in a short-distance migrant mosquito: Evidence for the dengue vector Aedes aegypti", PLoS Neglected Tropical Diseases, Vol. 4, No. 3: e634.
- Honório, N.A. et al. (2003), "Dispersal of Aedes aegypti and Aedes albopictus (Diptera: Culicidae) in an urban endemic dengue area in the state of Rio de Janeiro, Brazil", Memórias do Instituto Oswaldo Cruz, Vol. 98, pp. 191-198.
- Huber, K. et al. (2002), "Genetic differentiation of the dengue vector, *Aedes aegypti* (Ho Chi Minh City, Vietnam) using microsatellite markers", *Molecular Ecology*, Vol. 11, No. 9, pp. 1629-1635.
- Hutchinson, G.E. (1957), "Concluding remarks", Cold Spring Harbor Symposia on Quantitative Biology, Vol. 22, pp. 415-427.
- Jansen, C.C. and N.W. Beebe (2010), "The dengue vector Aedes aegypti: What comes next", Microbes and Infection, Vol. 12, pp. 272-279.
- Jetten, T.H. and D.A. Focks (1997), "Potential changes in the distribution of dengue transmission under climate warming", *The American Journal of Tropical Medicine and Hygiene*, Vol. 57, pp. 285-297.
- Juliano, S.A. and L.P. Lounibos (2005), "Ecology of invasive mosquitoes: Effects on resident species and on human", *Ecology Letters*, Vol. 8, pp. 558-574.

- Kay, B. and V.S. Nam (2005), "New strategy against *Aedes aegypti* in Vietnam", *Lancet*, Vol. 365, No. 9459, pp. 613-617.
- Klowden, M.J. and A.O. Lea (1978), "Blood meal size as a factor affecting continued host-seeking by Aedes aegypti (L.)", American Journal of Tropical Medicine and Hygiene, Vol. 27, pp. 827-831.
- Koenraadt, C.J.M. et al. (2008), "Spatial and temporal patterns in pupal and adult production of the dengue vector *Aedes aegypti* in Kamphaeng Phet, Thailand", *The American Journal of Tropical Medicine and Hygiene*, Vol. 79, pp. 230-238.
- Lambdin, B.H. et al. (2009), "Dry Season production of filariasis and dengue vectors in American Samoa and comparison with wet season production", *The American Journal of Tropical Medicine and Hygiene*, Vol. 81, pp. 1013-1019.
- Lenhart, A.E. et al. (2006), "Use of the pupal/demographic-survey technique to identify the epidemiologically important types of containers producing *Aedes aegypti* (L.) in a dengue-endemic area of Venezuela", *Annals of Tropical Medicine and Parasitology*, Vol. 100 (Supple. 1), pp. S1-S7.
- Liu-Helmersson, J. et al. (2016), "Climate change and *Aedes* vectors: 21<sup>st</sup> century projections for dengue transmission in Europe", *EBioMedicine*, Vol. 7, pp. 267–277.
- Lounibos, L.P. et al. (2002), "Does temperature affect the outcome of larval competition between Aedes aegypti and Aedes albopictus?", Journal of Vector Ecology, Vol. 27, pp. 86-95.
- Lounibos, L.P. (1981), "Habitat segregation among African treehole mosquitoes", *Ecological Entomology*, Vol. 6, pp. 129-154.
- Lozano-Fuentes, S. et al. (2012), "The dengue virus mosquito vector Aedes aegypti at high elevation in Mexico", The American Journal of Tropical Medicine and Hygiene, Vol. 87, No. 5, pp. 902-909.
- Maciel-de-Freitas, R., C.T. Codeço and R. Lourenço-de-Oliveira (2007a), "Daily survival rates and dispersal of Aedes aegypti females in Rio de Janeiro, Brazil", American Journal of Tropical Medicine and Hygiene, Vol. 76, No. 4, pp. 659-665.
- Maciel-de-Freitas, R., C.T. Codeço and R. Lourenço-de-Oliveira (2007b), "Body size-associated survival and dispersal rates of *Aedes aegypti* in Rio de Janeiro", *Medical and Veterinary Entomology*, Vol. 21, pp. 284-292.
- Maciel-de-Freitas, R. et al. (2006), "Movement of dengue vectors between human the human modified environment and an urban forest in Rio de Janeiro", *Journal of Medical Entomology*, Vol. 43, pp. 1112-1120.
- Mackenzie, J.S., D.J. Gubler and L.R. Petersen (2004), "Emerging flaviviruses: The spread and resurgence of Japanese encephalitis, West Nile and dengue viruses", *Nature Medicine*, Vol. 10, S98-S109.
- Magori, K. et al. (2009), "A stochastic, spatially explicit modelling tool for studying *Aedes aegypti* population replacement and population suppression strategies", *PLoS Negleted Tropical Diseases*, No. 3, No. 9, pp. 1-18.
- McDonald, P.T. (1977), "Population characteristics of domestic Aedes aegypti (DipteraL Culicidae) in villages on the Kenya coast: II. Dispersal within and between villages", Journal of Medical Entomology, Vol. 14, pp. 49-53.
- Mogi, M. (2007), "Insects and other invertebrate predators", Journal of the American Mosquito Control Association, Vol. 23, No. sp2, pp. 93-109.
- Morlan, H.B. and R.O. Hayes (1958), "Urban dispersal and activity of *Aedes aegypti*", *Mosquito News*, Vol. 18, pp. 137-144.
- Morrison, A.C. et al. (2008), "Defining challenges and proposing solutions for control of the virus vector Aedes aegypti", PLoS Medicine, Vol. 5: e68.
- Morrison, A.C. et al. (2004), "Temporal and geographic patterns of *Aedes aegypti* production in Iquitos, Peru", *Journal of Medical Entomology*, Vol. 42, pp. 502-510.
- Muir, L.E. and B.H. Kay (1998), "Aedes aegypti survival and dispersal estimated by mark-release-recapture in northern Australia", The American Journal of Tropical Medicine and Hygiene, Vol. 58, pp. 277-282.
- Murrell, E.G. and A.J. Steven (2008), "Detritus type alters the outcome of interspecific competition between *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae)", *Journal of Medical Entomology*, Vol. 45, No. 3, pp. 375-385.

- Nasci, R.S. (1991), "Influence of larval and adult nutrition on biting persistence in *Aedes aegypti* (Diptera: Culicidae)", *Journal of Medical Entomology*, Vol. 28, pp. 522-526.
- Nazri, C.D., A.H. Ahmad and R. Ismail (2013), "Habitat Characterization of Aedes Sp. Breeding in Urban Hotspot Area", Procedia - Social and Behavioral Sciences, Vol. 85, pp. 100-109.
- Ooi, E.E. and D.J. Gubler (2009), "Global spread of epidemic dengue: The influence of environmental change", *Future Virology*, Vol. 4, pp. 571-580.
- Ordóñez-Gonzalez, J.G. et al. (2001), "The use of sticky ovitraps to estimate dispersal of *Aedes aegypti* in northeastern Mexico", *Journal of the American Mosquito Control Association*, Vol. 17, No. 2, pp. 93-97.
- Otero, M., N. Schweigmann and H.G. Solari (2008), "A stochastic spatial dynamical model for Aedes aegypti", Bulletin of Mathematical Biology, Vol. 70, No. 5, pp. 1297-1325.
- Otero, M., H.G. Solari and N. Schweigmann (2006), "A stochastic population dynamics model for *Aedes aegypti*: Formulation and application to a city with temperate climate", *Bulletin of Mathematical Biology*, Vol. 68, No. 8, pp. 1945-1974.
- Packer, M.J. and P.S. Corbet (1989), "Size variation and reproductive success of female Aedes punctor (Diptera: Culicidae)", Ecological Entomology, Vol. 14, pp. 297-309.
- Patz, J.A. et al. (1998), "Dengue fever epidemic potential as projected by general circulation models of global climate change", *Environmental Health Perspectives*, Vol. 106, pp. 147-153.
- Pumpuni, C.B. and E.D. Walker (1989), "Population size and survivorship of adult Aedes triseriatus in a scrap tireyard in northern Indiana", Journal of the American Mosquito Control Association, Vol. 5, pp. 166-172.
- Raxworthy, C.J. et al. (2007), "Applications of ecological niche modelling for species delimitation: A review and empirical evaluation using day geckos (*Phelsuma*) from Madagascar", *Systematic Biology*, Vol. 56, No. 6, pp. 907-923.
- Reiter, P. et al. (1995), "Dispersal of Aedes aegypti in an urban area after blood feeding as demonstrated by rubidium-marked eggs", The American Journal of Tropical Medicine and Hygiene, Vol. 52, pp. 177-179.
- Renshaw, M., M.W. Service and M.H. Birley (1994), "Size variation and reproductive success in the mosquito *Aedes cantans*", *Medical and Veterinary Entomology*, Vol. 8, pp. 179-186.
- Reuben, R., M. Yasuno and K.N. Panicker (1972), "Studies on the dispersal of Aedes aegypti at two localities in Delhi", WHO/VBC/72.388, World Health Organization.
- Reyes-Villanueva, F. (2004), "Egg development may require multiple bloodmeals among small *Aedes aegypti* (Diptera: Culicidae) field collected in northeastern Mexico", *Florida Entomologist*, Vol. 87, pp. 630-632.
- Ritchie, S.A. (2014), "Dengue vector bionomics: Why *Aedes aegypti* is such a good vector", in D. Gubler et al. (eds), *Dengue and Dengue Hemorrhagic Fever*, CAB International, Oxfordshire.
- Rodhain, F. and L. Rosen (1997), "Mosquito vectors and dengue virus vector relationships", in D.J. Gubler, and G. Kuno (eds), *Dengue and Dengue Hemorrhagic Fever*, CAB International, New York, pp. 45-60.
- Rueda, L.M. et al. (1990), "Temperature-dependent development and survival rates of *Culex quinquefasciatus* and *Aedes aegypti* (Diptera. Culicidae)", *Journal of Medical Entomology*, Vol. 27, No. 5, pp. 892-898.
- Russell, R.C. et al. (2009), "Dengue and climate change in Australia: Predictions for the future should incorporate knowledge from the past", *Medical Journal of Australia*, Vol. 190, pp. 265-268.
- Russell, R.C. et al. (2005), "Mark-release-recapture study to measure dispersal of the mosquito Aedes aegypti in Cairns, Queensland, Australia", Medical and Veterinary Entomology, Vol. 19, pp. 451-457.
- Russell, B.M., B.H. Kay and W. Shipton (2001), "Survival of Aedes aegypti (Diptera: Culicidae) eggs in surface and subterranean breeding sites during the northern Queensland dry season", Journal of Medical Entomology, Vol. 38, pp. 441–445.
- Scott, T.W. et al. (2000), "Longitudinal studies of *Aedes aegypti* (Diptera: Culicidae) in Thailand and Puerto Rico: Population dynamics", *Journal of Medical Entomology*, Vol. 37, No. 1, pp. 77-88.
- Scott, T.W. et al. (1993), "Blood-feeding patterns of Aedes aegypti (Diptera: Culicidae) collected in a rural Thai village", Journal of Medical Entomology, Vol. 30, No. 5, pp. 922-927.

- Shaalan, E.A. and D.V. Canyon (2009), "Aquatic insect predators and mosquito control", *Tropical Biomedicine*, Vol. 26, No. 3, pp. 223-261.
- Sheppard, P. et al. (1969), "The dynamics of an adult *Aedes aegypti* in relation to dengue hemorrhagic fever in Bangkok", *The Journal of Animal Ecology*, Vol. 38, pp. 661-702.
- Strickman, D. and P. Kittayapong (2002), "Dengue and its vectors in Thailand: Introduction to the study and seasonal distribution of *Aedes* larvae", *American Journal of Tropical Hygiene and Medicine*, Vol. 67, pp. 247-259.
- Sulaiman, S. et al. (1990), "Detection of *Aedes aegypti* (L.) (Diptera: Culicidae) predators in urban slums in Malaysia using the precipitin test", *Mosquito Borne Diseases Bulletin*, Vol. 7, pp. 123–126.
- Suwonkerd, W. et al. (2006), "The effect of host type on movement patterns of *Aedes aegypti* (Diptera: Culicidae) into and out of experimental huts in Thailand", *Journal of Vector Ecology*, Vol. 31, pp. 311-318.
- Teng, H.J. and C.S. Apperson (2000), "Development and survival of immature Aedes albopictus and Aedes triseriatus (Diptera: Culicidae) in the laboratory: Effects of density, food, and competition on response to temperature", Journal of Medical Entomology, Vol. 37, No. 1, pp. 40-52.
- Trpis, M. (1973), "Interaction between the predator *Toxorhynchites brevipalpis* and its prey *Aedes aegypti*", *Bulletin of the World Health Organization.*, Vol. 49, No. 4, pp. 359.
- Trpis, M. and W. Hausermann (1986), "Dispersal and other population parameters of Aedes aegypti in an African village and their possible significance in epidemiology of vector-borne diseases", The American Journal of Tropical Medicine and Hygiene, Vol. 35, pp. 1263-1279.
- Trpis, M., W.O. Haufe and J.A. Shemanchuk (1973), "Embryonic development of *Aedes* (O.) *sticticus* (Diptera: Culicidae) in relation to different constant temperatures", *The Canadian Entomologist*, Vol. 105, pp. 43-50.
- Tun-Lin, W., B.H. Kay and A. Barnes (1995), "The premise condition index: A tool for streamlining surveys of *Aedes aegypti*", *American Journal of Tropical Medicine and Hygiene*, Vol. 53, pp. 591-594.
- Tun-Lin, W. et al. (2009), "Reducing costs and operational constraints of dengue vector control by targeting productive breeding places: A multi-country non-inferiority cluster randomized trial", *Tropical Medicine & International Health*, Vol. 14, pp. 1143-1153.
- Urdaneta-Marquez, L. et al. (2008), "Genetic relationships among Aedes aegypti collections in Venezuela as determined by mitochondrial DNA variation and nuclear single nucleotide polymorphisms", The American Journal of Tropical Medicine and Hygiene, Vol. 78, No. 3, pp. 479-491.
- Valerio, L. et al. (2012). "Dispersal of male Aedes aegypti in a coastal village in southern Mexico", American Journal of Tropical Medicine and Hygiene, Vol. 86, No. 4, pp. 665-676.
- Williams, C.R. et al. (2015), "Testing the impact of virus importation rates and future climate change on dengue activity in Malaysia using a mechanistic entomology and disease model", *Epidemiol. Infect*, pp. 1-9.
- Williams, C.R. et al. (2014), "Bionomic response of *Aedes aegypti* to two future climate change scenarios in far north Queensland, Australia: Implications for dengue outbreaks", *Parasites and Vectors*, Vol. 7, pp. 447.
- Williams, C.R. et al. (2013), "Productivity and population density estimates of the dengue vector mosquito Aedes aegypti (Stegomyia aegypti) in Australia", Medical and Veterinary Entomology, Vol. 27, pp. 313–322.
- Williams, C.R. et al. (2010), "The extinction of dengue through natural vulnerability of its vectors", *PLoS Neglected Tropical Diseases*, Vol. 4, No. 12: e922.
- Williams, C.R. et al. (2008), "Rapid estimation of *Aedes aegypti* population size using simulation modeling, with a novel approach to calibration and field validation", *Journal of Medical Entomology*, Vol. 45, No. 6, pp. 1173-1179.
- Xu, C. et al. (2010), "Understanding uncertainties in model-based predictions of *Aedes aegypti* population dynamics", *PLoS Neglected Tropical Diseases*, Vol. 4, No. 9: e830.
- Xue, R.D., J.D. Edman and T.W. Scott (1995), "Age and body size effects on blood meal size and multiple blood feeding by *Aedes aegypti* (Diptera: Culicidae)", *Journal of Medical Entomology*, Vol. 32, pp. 471-474.

- Yan, G., D.D. Chadee and D.W. Severson (1998), "Molecular population genetics of the yellow fever mosquito: Evidence for genetic hitchhiking effects associated with insecticide resistance", *Genetics*, Vol. 148, pp. 793-800.
- Yuval, B., J.W. Wekesa and R.K. Washino (1993), "Effect of body size on swarming behavior and mating success of male *Anopheles freeborni* (Diptera: Culicidae)", *Journal of Insect Behaviour*, Vol. 6, pp. 333-342.



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