24 Dengue Vector Bionomics: Why *Aedes aegypti* is Such a Good Vector

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Introduction

Dengue remains the leading arbovirus cause of morbidity in man. There are 3.6 billion people living in areas of dengue risk, with an estimated 390 million infections and 96 million symptomatic cases annually (Beatty *et al.*, 2009, Bhatt *et al.*, 2013). Dengue is vectored by mosquitoes, with several members of the *Aedes Stegomyia* subgenus serving as vectors. For example, *Ae. albopictus* is an excellent vector of dengue in the laboratory, and outbreaks in Hawaii (Effler *et al.*, 2005) and Taiwan (Lambrechts *et al.*, 2010) attest to their ability to vector the virus in the field. Differences in the ability for *Ae. albopictus* to develop disseminated infections of dengue viruses may explain its lower vector competence status relative to *Ae. aegypti* (Lambrechts *et al.*, 2010). *Ae. scutellaris* complex members *Ae. polynesiensis* (Rosen *et al.*, 1954), *Ae. katheriensis* (Leake, 1984) and *Ae. scutellaris* (Moore *et al.*, 2007) have been shown to be potential vectors of dengue virus in the laboratory. *Ae. polynesienis* is suspected of vectoring outbreaks in French Polynesia (Rosen *et al.*, 1954), while *Ae. hensilli* (Savage *et al.*, 1998) and *Ae. scutellaris* (Mackerras, 1946) have been linked to dengue transmission in Yap and New Guinea, respectively. However, it is another *Aedes* (*Stegomyia*) spp., *Ae. aegypti*, that is responsible for the bulk of dengue transmission worldwide – and is almost exclusively the vector in large, explosive urban epidemics of dengue (Gubler, 1998; Lambrechts *et al.*, 2010). What is unique about *Ae. aegypti* that makes it such an effective vector of dengue?

Ae. aegypti is arguably the most anthropophilic mosquito (Tabachnick, 1991). Most of its behavior – from immatures residing within man-made, water-holding containers to adult females living inside human domains where they feed almost exclusively on human blood – is tightly linked to man. Its high domesticity truly makes *Ae. aegypti* the 'cockroach' of mosquitoes, and contributes greatly to its capacity to vector dengue. This chapter will describe *Ae. aegypti*'s close association with man based on the published scientific literature tempered with my own personal experience with the mosquito: I have lived in an unscreened Queenslander house where *Ae. aegypti* are encountered almost daily, and have directed the dengue control program in north Queensland, Australia for Queensland Health from 1994 to 2010. For an excellent discussion of the evolution of anthropophily in mosquitoes, especially the malaria vector *Anopheles gambiae s.s.*, see Costantini *et al.* (1999).

Adult Behavior

Blood feeding

Nearly exclusive blood feeding on humans drives *Ae. aegypti*'s role as principal vector

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of dengue and yellow fever (Lambrechts *et al.*, 2010). Mosquitoes that feed almost exclusively on man, such as *An. gambiae s.s.* (Besansky *et al.*, 2004; Lefèvre *et al.*, 2009) and *Ae. aegypti*, maintain their respective pathogens within a tight, efficient mosquito–man transmission cycle (Lambrechts *et al.*, 2010). Blood-meal analysis studies have shown that *Ae. aegypti* feeds predominantly on man in Puerto Rico (Scott *et al.*, 2000b), Thailand (Scott *et al.*, 1993, 2000b; Ponlawat and Harrington, 2005) and Cairns (Jansen *et al.*, 2009). This selective feeding on human blood, at the expense of animal blood, plant nectar and fruit juice, is thought to be associated with greater egg production after imbibing isoleucine-poor human blood (Harrington *et al.*, 2001). Reliance on blood rather than fructose for metabolic energy necessitates repeated blood feeding on an almost daily basis (Scott *et al.*, 2000a; Harrington *et al.*, 2001).

This repeated blood feeding on man along with a relatively high daily survival (Reiter, 2007) collectively contributes to the capacity for *Ae. aegypti* to cause explosive epidemics of dengue and yellow fever in urban areas. Most mosquitoes have a daily survival of <0.9 per day (Clements and Paterson, 1981). Reiter (2007) reports on several studies that, using the length of the gonotrophic cycle, the time between successive oviposition events, estimate the daily survival of female *Ae. aegypti* as 0.91 to 0.93. Critically, oviposition, and thus the gonotrophic cycle, is extended over several days as females skip oviposit at many sites. This extended gonotrophic cycle mathematically increases daily survival estimates (Reiter, 2007). By surviving longer, infected females can bite more hosts, transmitting virus to a greater number of susceptible humans. However, multiple blood feeding and skip oviposition may confound measurements of the length of the gonotrophic cycle, and thus estimates of age in *Ae. aegypti*. Clearly, more direct methods to measure mosquito age, such as proteins and gene expression (Cook *et al.*, 2007; Hugo *et al.*, 2010), need further development and refinement.

The intensive biting activity on man exposes female *Ae. aegypti* to host defensive behavior such as swats and slaps as the host attempts to kill or disperse the attacking female. Thus, female *Ae. aegypti* have evolved to preferentially feed on the lower limbs and feet, which are physically farthest away from swatting hands. There is evidence that these areas are exceptionally rich in lactic and carboxylic acids created by bacteria interacting with human eccrine sweat, and that these compounds are especially attractive to both *An. gambiae s.s* and *Ae. aegypti* in olfactometer experiments (Smallegange *et al.*, 2011). *Ae. aegypti* are also extremely nervous feeders, alighting at the slightest movement, only to preferentially attack again (Lenahan and Boreham, 1976). Thus, because female *Ae. aegypti* continue blood feeding until a nearly full blood meal is obtained (Klowden and Lea, 1978), they are persistent biters (Canyon *et al.*, 1998) and often take several partial blood meals within a house and within a day (Scott *et al.*, 2000a).

Adult harborage

Much of the basic key behavioral activities of *Ae. aegypti* take place within or near the house. *Ae. aegypti* also preferentially reside, and are attracted to, buildings where humans reside (Reiter and Gubler, 1997; Perich *et al.*, 2000). In an elegant study, Suwonkerd *et al.* (2006) examined the exit and entry of female *Ae. aegypti* to huts containing humans, a dog and an unbaited control. Female *Ae. aegypti* not only preferred to enter huts with humans, but they also significantly remained in such huts. Within a premise, *Ae. aegypti* preferentially rest in dark, shady areas (Schoof, 1967). Reiter and Gubler (1997) describe *Ae. aegypti* as a furtive, skulking insect that spends much of its time sequestered in heavily sheltered indoor refuges that are devoid of air movement. The preferential attraction of both male and female *Ae. aegypti* to black, red and dark shades is well known (Muir *et al.*, 1992a,b), and likely reflects mosquito attraction to the microclimate of dark, shady areas – minimal wind, cooler temperatures and high humidity – that would minimize desiccation to resting insects (Fig. 24.1). The selective insecticidal spraying of dark objects likely to harbor resting *Ae. aegypti* has been used to successfully control *Ae. aegypti* and stop dengue transmission (Ritchie *et al.*, 2002;

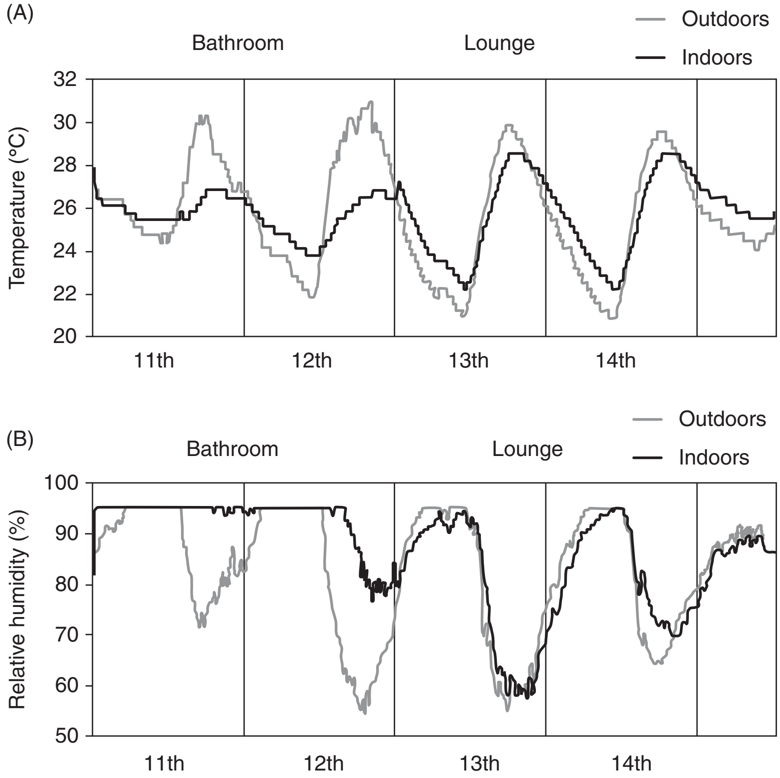

Fig. 24.1. Microclimates within a 'Queenslander house'. Data logger readings were taken with an Esis Hygrocon DS1923 (Esis Pty Ltd, PO Box 450, Pennant Hills NSW 1715, Australia) at height of 0.3 m; relative humidity readings were capped at 95%. (A) Recordings of temperature and (B) relative humidity were made within a ground floor bathroom on 11–12 November 2007 and adjacent downstairs lounge room on 13–14 November 2007. Outdoor readings were taken in undercover ground floor area within 1 m of the house. The bathroom was dark and poorly ventilated, with a porous tile floor that absorbed moisture, increasing humidity while reducing temperature fluctuations. Such dark, still locations minimize desiccation and are sought out by adult *Ae. aegypti* for harborage sites.

Vazquez-Prokopec *et al.*, 2010). Male *Ae. aegypti* aggregate on dark objects inside premises (Reiter and Gubler, 1997), and are also attracted to humans where they may intercept and copulate with females (Hartberg, 1971). They may also encounter females at other domestic locations including oviposition sites and resting sites (Hartberg, 1971; Ponlawat and Harrington, 2009).

Adult flight behavior

Ae. aegypti flight behavior ensures that they remain close to humans and, literally, proximal to blood-meal sources, harborage areas and oviposition sites. This is in contrast to dispersal behavior exhibited by many other mosquitoes, some of which are renowned for long-distance flight and migration. The primary saltmarsh mosquitoes of Florida and Australia, *Ae. taeniorhynchus* (Ritchie and Montague, 1995; Vlach *et al.*, 2006) and *Ae. vigilax* (Ritchie, 1993), respectively, engage in long dispersive flights of up to tens of kilometers from their larval habitat. The Japanese encephalitis vectors *Culex tritaeniorhynchus* and *Cx. annulirostris* are also known to fly, at height, over considerable distances (van den Hurk *et al.*, 2009). However, *Ae. aegypti* typically fly only a few hundred meters, often less (Harrington *et al.*, 2005; Russell *et al.*, 2005). This ensures that they stay near human habitats, facilitating house-to-house flights in search of blood-meal or oviposition sites, where they may aggregate (Edman *et al*., 1998). Furthermore, low-level flight prevents the adult mosquito from flying above the wind boundary layer above which wind speed can increase dramatically (Srygley and Dudley, 2008), potentially sweeping small insects away to unsuitable habitats.

Adult flight distance and dispersal

Estimation of the flight distance of *Ae. aegypti*, and indeed, *Ae. albopictus*, is fraught with controversy and inconsistency. The dispersal distance is largely a function of time; distance travelled in a day will be considerably smaller than that travelled in a week. The maximum distance travelled is often defined by the distance traps are set from the release site. Obviously, in many studies, the measured maximum distance travelled will be up to the outer boundary of traps. Contributing to this are the geographic confines of the release area. For instance, Harrington *et al.* (2005) conducted mark–release–recapture (MRR) within small villages confined by rice paddies and limestone cliffs; obviously *Ae. aegypti* were restricted to the boundary of the urban terrain. So, we really need to look at *Ae. aegypti* dispersal with a large, contiguous urban area, within a realistic time frame such as within the extrinsic incubation period (EIP) of dengue virus (ca. 10 days). The study by Reiter *et al.* (1995) was conducted in an urban area of San Juan, Puerto Rico, but only included time to oviposition. None the less, female *Ae. aegypti* travelled up to 400 m from the release point. Other studies have used release methods that could artificially impact dispersion. Perhaps the most obvious are the studies that employed proboscal amputation (Shirai *et al.*, 2000) or glue (Liew and Curtis, 2004) to prevent blood feeding and eliminate risk of dengue transmission by released mosquitoes. *Ae. aegypti* feed almost exclusively on human blood, often daily (Scott *et al.*, 2000a,b), and ‘gagged’ mosquitoes would probably desperately disperse in search of a host that they could never feed upon, and traverse greater distances than normal. Furthermore, Bellini *et al.* (2010) found that male *Ae. albopictus* dusted with fluorescent powders had significantly reduced recovery and distance travelled compared to undusted male *Ae. albopictus* ‘marked’ by clearing of naturally occurring *Wolbachia* infections by antibiotics. Granted these were male *Ae. albopictus*, but the questions raised would also apply to females *Ae. aegypti* as well.

Clearly a method that measures natural dispersion of *Ae. aegypti* within a contiguous urban environment over an epidemiologically significant period are needed. Vazquez-Prokopac *et al.* (2010) used an elegant GIS method to quantify the wave of dengue transmission from a point source inoculation (patient zero) over the first and second rounds of transmission in an urban area of Cairns, Australia. While many dengue cases would be spread via human movement, this would be rather random and distant and easily distinguished from the concentrated wave of cases that radiated locally from the index case. The transmission wave would have been largely driven by the dispersal of female *Ae. aegypti* from houses nearby the index case, which were present in high numbers in the area (Ritchie *et al.*, 2004; Hanna *et al.*, 2006). This ‘pebble in the pond’ wave analysis indicated that *Ae. aegypti* dispersal from the introduction point within the 2-week EIP time frame (the dispersal kernel) was elliptical (ca. 100 × 300 m), described by the 3 × 1 rectangular urban block dimension of the area (Vazquez-Prokopec *et al.*, 2010). The average movement within 2 weeks was 80 m away from the index case, with ca. 95% of cases within 200 m. Case distribution occurred equally up and down to the prevailing southeasterly winds, suggesting mosquito movement was not significantly impacted by surface winds. Similar analysis of a 2008 ‘pebble in the pond’ dengue event in a Cairns urban area with a square (1 × 1) block dimension found that the dengue cases and thus potential mosquito dispersion were uniformly distributed around the index case (Vazquez-Prokopec personal communication), supporting the dispersion relationship found in 2003. These observations suggest that *Ae. aegypti* movement is largely house-to-house. This confirms the observations of Harrington *et al.* (2005), based on 21 MRR studies, that female *Ae. aegypti* generally remain within the release house or adjacent houses. Thus, it appears that female *Ae. aegypti* will apparently travel down or upwind, perhaps in response to changing wind directions over the period, or to changing cues such as those provided by shade, oviposition sites and human kairomones including CO_2. When provided with a choice of crossing a street or flying to an adjacent house, the female will choose the house. Larger roads have been identified as significant barriers to gene flow, and thus dispersal, of *Ae. aegypti* in Trinidad (Hemme *et al.*, 2010), and to dispersal in Cairns, Australia (Russell *et al.*, 2005). The release of large numbers of *Wolbachia*-infected *Ae. aegypti* (Hoffmann *et al.*, 2011) that serve as a unique marker will offer an excellent opportunity to measure intra and intergenerational dispersal of *Ae. aegypti*, as well as adult survival and population size (Ritchie *et al.*, 2013).

Exploiting the Opportunities Offered by Artificial Containers

Oviposition activities are also tightly linked to man. Indeed, exploitation of man-made larval habitats has been given as a major driver of anthropophily in mosquitoes: ‘The association to those humans acting as the producers of breeding sites, thus exploited by mosquitoes both as hosts and as a guide for breeding opportunities’ (Costantini *et al.*, 1999, p. 213). *Ae. aegypti* is among a group of mosquitoes commonly referred to as container ‘breeding’ mosquitoes, mosquitoes that lay their eggs in objects with firm sides that hold water. (Clearly container ‘breeding’ is a misnomer, because mating does not take place within the flooded containers. I prefer and will use the terms container-inhabiting or container-exploiting.) So, earthen water-holding bodies such as puddles, ponds, ditches, drains and swamps do not attract oviposition by *Ae. aegypti*. But natural containers, such as tree holes, fallen palm fronds, dead open coconuts and phytotelmatic plants such as bromeliads can be used, and indeed may represent ancestral larval habitat. But it is generally agreed that artificial containers made of plastic, fiberglass, wood, concrete, porcelain, metal, etc. represent the majority of oviposition and larval habitats. Containers producing *Ae. aegypti* have been categorized by their use, shape and composition (Barker-Hudson *et al.*, 1988; Koenraadt *et al.*, 2007). Oviposition is proportional to the water-holding volume and diameter of the container opening (Harrington *et al.*, 2008), although oviposition is reduced for the largest containers (Wong *et al.*, 2011). *Ae. aegypti* biology often reflects cultural differences between peoples. For example, the ornate ceramic water storage jars used in much of Southeast Asia are a key container for *Ae. aegypti* (Southwood *et al.*, 1972; Knox *et al.*, 2007), while rainwater tanks are a key container in the Torres Strait of Australia (Hanna *et al.*, 1998). Oviposition sites are often highly aggregated in space and time, and premises that contain a disproportionate number of production sites are referred to as key premises (Tun-Lin *et al.*, 1995; Chadee, 2004) or super-producers (Padmanabha *et al.*, 2012). Obviously, the exploitation of man-made water holding vessels enabled *Ae. aegypti* to share human households, as well as travel with him during expanding trade from Africa to the Americas and Southeast Asia (Tabachnick, 1991; Brown *et al.*, 2011). To this day, *Aedes* mosquitoes are still travelling the world in water-holding drums and cargo on container ships and fishing vessels (Shortus and Whelan, 2006).

Attributes of *Ae. aegypti* that enable it to exploit artificial containers

The capacity for *Ae. aegypti* to exploit man-made containers relies upon several key attributes of the mosquito. First, they must be able to locate small, often isolated containers that may hold but a cupful of water, containers with an opening the size of your thumb, and containers cryptically located under houses or 10 m in the air. Second, the larvae must be able to successfully compete for the limited amount of nutrients that fall through the small opening of the container. These larvae must be able to survive long stints of starvation when minimal food is available. Third, the mosquito must be able to rapidly exploit new containers as they are created by man, or flooded by rain, before they too become overcrowded. And finally, the eggs must be able to survive long periods of dry weather when containers dry out. I will discuss each of the essential abilities in turn.

Location of oviposition sites

Insects have an amazing ability to locate key habitats using chemical cues. *Ae. aegypti* can locate and oviposit within quite small containers that are extremely isolated in their distribution. In drier areas of north Queensland, Australia, manhole service pits can house thousands of larvae, yet they have a surface opening consisting of a few 2 × 4 cm keyholes (Kay *et al.*, 2000; Russell *et al.*, 2002). Other cryptic sites known to produce *Ae. aegypti* include: elevated sites such as roof gutters (Montgomery and Ritchie, 2002), rainwater tanks (Hanna *et al.*, 1998), cisterns (Chandler, 1945) and bamboo pole holders in buildings (Ooi, 2001); subterranean sites such as sump pits (Montgomery *et al.*, 2004), septic tanks (Burke *et al.*, 2010), wells and buried cisterns (Chandler, 1945); and domestic appliances such as air-conditioner, refrigerator and wine-cabinet drip trays and meat safes. Furthermore, these cryptic larval habitats apparently attract and recruit ovipositing females through chemical cues. In north Queensland, service manholes with larvae tended to remain positive; indeed positive sites had a 96% probability of remaining positive in subsequent surveys several months later, while in negative sites the probability of becoming positive was only 1% (Kay *et al.*, 2000). This may be due, in part, to later hatching of large egg banks, but also suggests that ovipositing females are attracted to cues produced by conspecific larvae and pupae. A similar trend was found in Iquitos, Peru where oviposition was significantly greater in containers populated by conspecific larvae and pupae (Wong *et al.*, 2011). *Ae. aegypti* females can also locate nutrient-rich water, and this ability has been used to create plant-based infusions that enhance ovitrap collections (Reiter *et al.*, 1991; Ritchie, 2001). These infusions create a rich bacterial flora that act as a powerful attractant and ovipositional stimulant for *Ae. aegypti* (Ponnusamy *et al.*, 2008, 2010). The relative attraction of plant infusions can also vary with the age of the infusion and the species of plant used to create the infusion (Sant'ana *et al.*, 2006).

Life in a small world: containers and larval survival

The attraction and exploitation of conspecific attraction to larval habitat creates a dilemma. On one hand, it attracts ovipositing females to sites with a history of production – containers that hold water and contain sufficient nutrients for larval maturation (Wong *et al.*, 2011). On the other hand, strong conspecific oviposition attractants can lead to super oviposition and more larvae than the nutrients of the container can support. In order to spread the risk, gravid *Ae. aegypti* frequently engage in 'skip oviposition' and lay eggs in multiple containers (Colton *et al.*, 2003; Reiter, 2007). Despite this, overcrowding within containers occurs. Density-dependent regulation, created by strong competition for the limited food within the container, will lead to malnutrition, larval stunting and potentially starvation and death (Legros *et al.*, 2009; Reiskind and Lounibos, 2009). Field observations suggest that ovipositional kairomones exist (Wong *et al.*, 2011), so the benefits of locating and ovipositing in a flooded container must outweigh the costs of density-dependent regulation on larvae. Furthermore, models theoretically support this; sensitivity analysis of simulation models and life tables of mosquitoes indicate that model output (usually production of adult females) is most sensitive to adult female mortality rather than larval mortality (Dye, 1984; Ellis *et al.*, 2011).

Ae. aegypti have adapted to maximize production within the confined, nutrient-limiting environment. When resources are scarce, and larval densities high, larvae can become delayed, resulting in 'stacking' of late instar larvae. Pupal production in flooded containers can be relatively stable (Williams *et al.*, 2013), suggesting populations in containers are at their carrying capacity. Interestingly, in Vietnam, *Ae. aegypti* pupal production in earthenware jars used for domestic water storage was typically low, with periodic, episodic pulses of high pupation seemingly at random

(Jeffery *et al.*, 2009). It could be that a nutrient pulse, perhaps consisting of an insect or animal cadaver, or even a chicken bone tossed in by a child, suddenly gifted the massed *Ae. aegypti* a nutritional escape route from the jar. I have witnessed *Ae. aegypti* larvae skeletonize the cadaver of a cane toad (*Bufo marinus*) that was trapped in a bucket within a few days, leading to a surge in pupation. Even if larvae are nutritionally deprived, pupation can still occur, although adults are stunted (Chadee *et al.*, 2002); wing lengths of wild *Ae. aegypti* are usually considerably smaller, and often cover a wide range of sizes than those of laboratory *ad-libitum* reared *Ae. aegypti* (Reiskind and Lounibos, 2009). And at the extreme end, *Ae. aegypti* larvae will cannibalize conspecific larvae that succumb to starvation, or even prey on young instars (Edgerly *et al.*, 1999). Thus, despite overcrowding in the nutrient-limited environment of the container, *Ae. aegypti* larvae are able to survive lengthy periods of starvation, then exploit the slightest nutrient pulse to pupation.

But what are the costs of not being able to locate an oviposition site? If a suitable larval habitat cannot be found, no eggs will be laid at all. Furthermore, the often isolated, cryptic nature of sites suggests that it would be very difficult for a female to locate flooded containers by vision alone. While many of us remember the LBJs (little black jars) we used as oviposition traps, container color did not significantly affect oviposition, while container size (water volume, diameter of opening) did in a field study in Thailand (Harrington *et al.*, 2008). Long flights spent in search of an oviposition site expose the gravid female to predation and, especially, desiccation. Indeed, in dry areas such as Charters Towers, Queensland and Tucson, Arizona, flooded surface containers will be rare, and afternoon temperatures are high, with low humidity. The ability to rapidly locate oviposition sites such as wells and manholes will offer great selective advantage. Machado-Allison and Craig (1972) and Mogi *et al.* (1996) examined survival of adult females to varying humidity and found large differences between strains, suggesting this trait is heritable (Kearney *et al.*, 2009).

Shuttle oviposition and exploitation of wet- and dry-season containers

Ae. aegypti can also rapidly exploit new containers created by artificial flooding (such as flooded water drums, flower vases) or by rainfall. Indeed, the CDC-enhanced ovitrap uses paired ovitraps containing 10% and 90% hay infusion to induce oviposition by gravid *Ae. aegypti* within a 24-hour period (Reiter *et al.*, 1991). Monsoonal climates, by definition, have a pronounced wet and dry season. During the dry season, rainfall can be almost nonexistent, and only containers flooded artificially (flower vases, striking plant containers, drums) or containing large volumes of water and protected from evaporation (rainwater tanks, cisterns, wells, septic tanks) are actively producing *Ae. aegypti* (Chandler, 1945; Kay *et al.*, 2000; Chadee *et al.*, 2002; D. Gubler, unpublished data) (Fig. 24.2A). Surface containers are generally dry. However, the onset of heavy monsoonal rains floods surface containers, opening up a new niche that *Ae. aegypti* rapidly exploits (Fig. 24.2B) (Chadee, 2004). Thus, *Ae. aegypti* populations typically exhibit a bimodal pattern with markedly higher populations in the wet season (Fig. 24.3) (Chandler, 1945; Focks *et al.*, 2007; Azil *et al.*, 2010; Kumari *et al.*, 2011; and see Fig. 2 in Williams *et al.*, 2010). Conversely, in areas that have a continuous high rainfall with no prolonged dry season, e.g., Iquitos, Peru, the majority of pupae came from outdoor, rain-filled containers and production was high throughout the year (Morrison *et al.*, 2004, 2006). In areas where water storage containers are continuously flooded and highly productive, such as ceramic jars in Thailand and Vietnam, adult *Ae. aegypti* populations can remain high year-round (Southwood *et al.*, 1972; Jeffrey *et al.*, 2009). Targeting key dry-season containers before they expand into myriad surface containers during the wet has even been proposed as a strategy to control *Ae. aegypti* (Chandler, 1945; Kay *et al.*, 2002b). Within a short time period, such as a month into the wet season, they must be able to locate newly flooded containers as old receptacles are removed and new ones created. This especially relates to small surface containers such as plastic take away food containers and ice cream containers, or palm fronds (S. Ritchie, unpublished data).

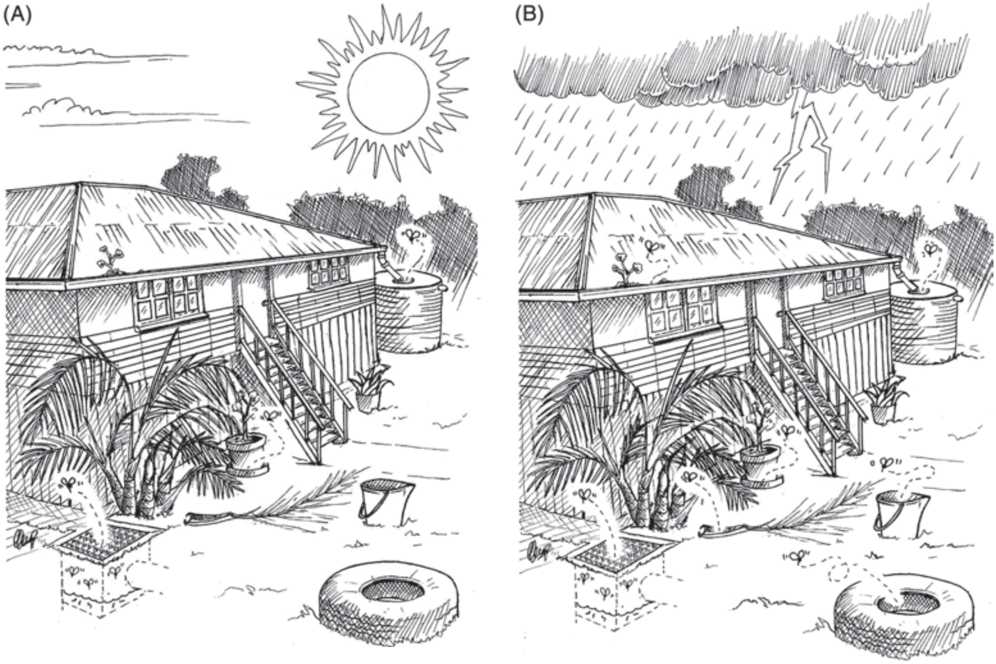

Fig. 24.2. Dry and wet season production in a typical north Queensland yard. During the dry season (A) flooded containers and *Ae. aegypti* production is limited to subterranean sites: sump pit, water storage units, rainwater tank and artificially flooded containers such as pot plant base. Upon resumption of the wet season (B), rain fills surface containers, palm fronds, roof gutters, buckets and tires that *Ae. aegypti* rapidly colonize, boosting production of adults.

The ability to rapidly exploit newly flooded, ephemeral containers allows *Ae. aegypti* to avoid many aquatic predators. Fish (Ghosh *et al.*, 2011) and many aquatic predaceous insects such as dragonfly naiads (Sebastian *et al.*, 1990) and backswimmers (Ellis and Borden, 1970) can predate *Ae. aegypti*, but generally populate established water bodies such as pools, ponds and swamps, and are usually artificially introduced for control in water storage containers. Perhaps the most innate predator of *Ae. aegypti* larvae are mosquitoes of the genus *Toxorhynchites*, whose adult females similarly seek out and exploit the same flooded artificial containers, such as tires and buckets, used by *Ae. aegypti* (Focks *et al.*, 1982).

The capacity of *Ae. aegypti* to exploit artificial containers enables it to maintain populations in times of low rainfall. Many of the classic 'key containers' (Tun-Lin *et al.*, 1995) for *Ae. aegypti* are artificially flooded sites used to store water, and produce large numbers of pupae even when rainfall is low (Table 24.1).

Survival of eggs in dry times

Finally, the production of desiccation-resistant eggs ensures *Ae. aegypti* survival over long periods (several months) of low rainfall and have contributed to its spread. Eggs have been shown to survive for several months, allowing populations to persist as eggs in dry environments before the onset of wet season rains (Focks *et al.*, 1993; Russell *et al.*, 2001; Juliano *et al.*, 2002). This capacity is likely to have a strong selective advantage (Kearney *et al.*, 2009; Williams *et al.*, 2010). Mosquito eggs are subject to predation, and long-term survival within a container would necessitate either a large egg bank to ensure some eggs survive, or the physical or chemical 'hiding' of eggs to avoid predation. Few studies have been done on predation of *Ae. aegypti* eggs.

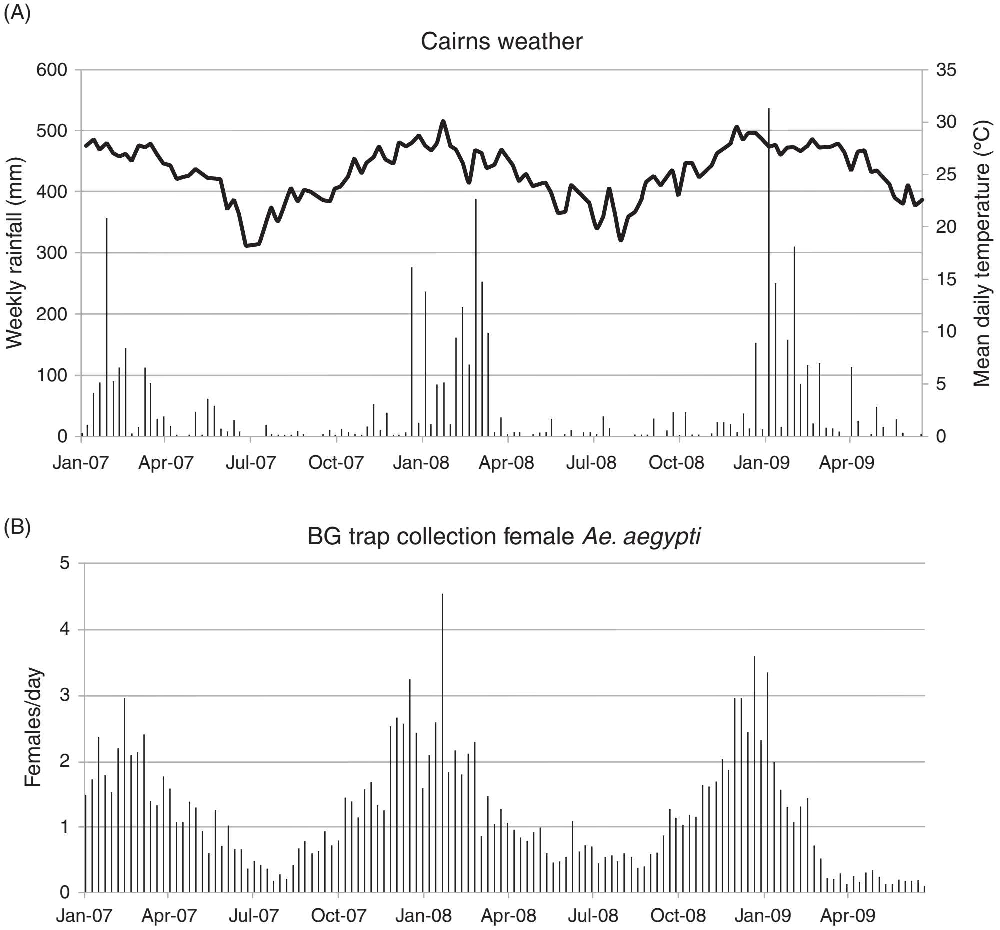

Fig. 24.3. Annual cycles of rainfall, temperature (A) and adult female *Ae. aegypti* (B) in Cairns, Australia. Adult *Ae. aegypti* mean females per trap day, using 13 traps collected weekly increase in response to higher temperatures in October–November, peaking with heavy rains from December to March.

Russell *et al.* (2001) placed filter-paper strips containing *Ae. aegypti* eggs within flooded telecommunication pits and surface containers in Charters Towers, Australia, and found that 0 and 1% of subterranean- and surface-placed eggs, respectively, survived the 4-month dry season. Predation was primarily by cockroaches. Attack by 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 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). *Ae. aegypti* can also directly oviposit on the water surface to avoid egg predation (Fig. 24.4). These eggs are held by water surface tension until embryonated, then hatch. This strategy would explain the constant cycling of generations within the subterranean sites that are subject to heavy predation on eggs laid on walls that none the less maintain the high larval/pupal populations (Russell *et al.*, 2002).

Table 24.1. Selected key containers for *Aedes aegypti*. These artificial containers have been shown to produce significant numbers of larvae/pupae and are common enough to warrant singling out.

Category	Composition	Location	References
I. Domestic water storage			
Jars (50–200 liters)	Ceramic, earthenware	Vietnam, Indonesia, Thailand, much of Southeast Asia	Knox *et al.* (2010); Koenraadt *et al.* (2008); Southwood *et al.* (1972)
Water tanks	Concrete	Vietnam	Kay *et al.* (2002a)
Cistern	Wooden, concrete	SE USA; Caribbean, Mediterranean (historical)	Chandler (1945); Curtin (1967); Christophers (1960)
Rainwater tank	Galvanized tin, fiberglass	Australia, Torres Strait	Tun-Lin *et al.* (1995); Hanna *et al.* (1998)
Drum	Metal, plastic	Caribbean, Indonesia, South Pacific	Chadee (2004); Shortus and Whelan (2006)
II. Domestic/industrial use			
Septic tank	Concrete, fiberglass	Puerto Rico	Burke *et al.* (2010); Mackay *et al.* (2009)
Evaporative coolers	Metal	India, USA	Batra *et al.* (2000); Halstead (2008)
Toilet water closet Bak mandi	Porcelain	Indonesia	Focks *et al.* (2007)
Ant trap	Ceramic, plastic	Indonesia, Southeast Asia	Southwood *et al.* (1972)
Plant striking container	Plastic	Australia, Torres Strait	Hanna *et al.* (1998)
Pot plant base	Plastic, ceramic	Australia	Hanna *et al.* (2006); Williams *et al.* (2008)
Sump pit	Concrete	Australia	Montgomery *et al.* (2004)
Flower pot, vase	Variety	Trinidad, Caribbean, Asia, Pacific	Focks and Chadee (1997)
Manhole service pit	Concrete	Australia	Kay *et al.* (2000); Russell *et al.* (2002)
Roof gutter	Aluminum	Australia	Montgomery and Ritchie (2002)
III. Miscellaneous rain-filled containers			
Boat	Aluminum	Australia, Torres Strait	S. Ritchie, unpublished data
Tarp/plastic sheeting	Plastic	Australia, Puerto Rico	Williams *et al.* (2008); Barrera *et al.* (2006)
Bucket	Plastic	Several	Barrera *et al.* (2006); Williams *et al.* (2008)
Tire	Rubber	Several, all tropics	Stoler *et al.* (2011); Hanna *et al.* (2001); Christophers (1960)

Why *Ae. aegypti* Populations are Low

As we have seen, several factors contribute to *Ae. aegypti*'s capacity to exploit and survive in the harsh environment of artificial containers. Some of these factors also contribute to the population dynamics of the species in nature. Generally speaking, *Ae. aegypti* populations are low, certainly much lower than the extreme populations that are observed in common floodwater *Aedes*, saltmarsh *Aedes* and pastureland *Culex*, where CDC trap collections often number into the 10,000 plus range. *Ae. aegypti*, on the other hand, are typically collected in single digits from infested

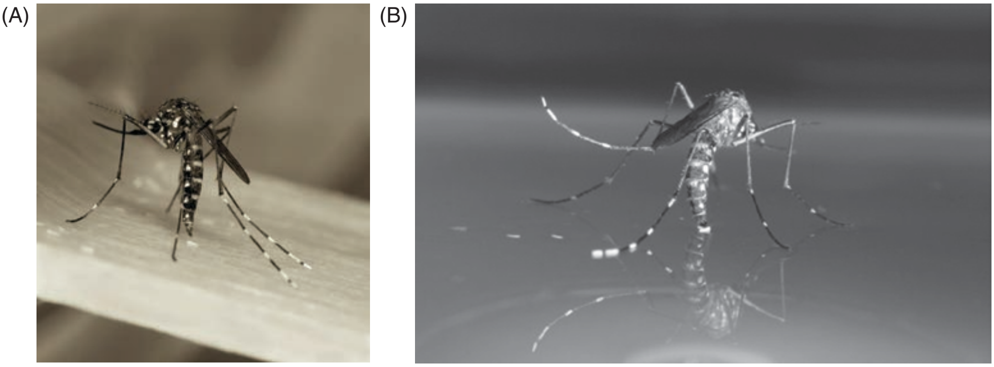

Fig. 24.4. Female *Ae. aegypti* ovipositing on wooden paint paddle (A) and on the water surface (B). Could alternative oviposition on water account for the large populations of larvae in subterranean containers where predation of eggs laid on the walls of subterranean pits by cockroaches is high (Russell *et al.*, 2001)?

houses. Adult population estimates, derived from MRR studies, pupal surveys and model estimates, are relatively small. Pupal surveys find that the pupae per person ranges from 0.34 to 22.7 in dengue-endemic or dengue-susceptible areas in the Caribbean, Central America and Southeast Asia (Focks *et al.*, 2000). Thus, assuming that pupal production is relatively stable (Williams *et al.*, 2013), 50% of the pupae are females, and that the daily survival of adult females is 0.89 (Focks *et al.*, 2000), integrating across all age groups provides an estimated range of 1.5–100 females per person. This equates to an estimated 6 to just over 400 for a typical household size of 4 people (Jennings *et al.*, 1999). Why are *Ae. aegypti* populations relatively low? Obviously, the overall volume and area of larval habitat is low relative to a 500 ha saltmarsh. An *Ae. aegypti*-infested neighborhood might only have 1–3 larval sites per house, producing 4–10 pupae per day. Furthermore, nutrients in the containers, as we have seen, limit production within each container. While potential larval habitat is associated with higher overall levels of production (Aldstadt *et al.*, 2011), often many containers remain '*aegypti* free', and do not produce *Ae. aegypti*.

Clearly there is some other limiting factor beyond larval habitat. Because *Ae. aegypti* feed almost exclusively on man, the abundance of water-filled containers created by humans are significantly associated with *Ae. aegypti* production (Aldstadt *et al.*, 2011). In Arizona, *Ae. aegypti* density, measured using ovitraps, was significantly associated with house age, with older homesteads having higher ovitrap counts (Walker *et al.*, 2011). Access to humans is also a limiting factor. In the USA, most houses are screened to exclude insects. Screened, air-conditioned housing was found to dramatically reduce the incidence of dengue in Laredo, Texas relative to neighboring Nuevo Laredo and Tamaulipas in Mexico, where houses were not screened (Reiter *et al.*, 2003). The contemporary household environment often contains an array of commercially available insecticides. Fly sprays, surface sprays, plug-in zappers and mosquito coils all contain synthetic pyrethroid insecticides and, in response to the nuisance of biting *Ae. aegypti* inside households, are probably often used to kill adult *Ae. aegypti*. Thus, part of the key of *Ae. aegypti*'s success has been its repeated ability to develop physiological resistance to pyrethroids (Hemingway and Ranson, 2000; Ponlawat *et al.*, 2005) and the organophosphates (e.g. temephos) (Seccacini *et al.*, 2008) used in water storage jars. This has resulted in high levels of genetic differentiation in *Ae. aegypti* urban areas as local extinction events and selection for resistant genotypes ensues (Paupy *et al.*, 2000; Ocampo and Wesson, 2004).

A Little Bit on Males

Male *Ae. aegypti* are also closely linked to human habitat. Unfortunately, because they do not bite, have little role in DENV transmission, and are not collected in traps such as ovitraps, male *Ae. aegypti* have been poorly studied (Ponlawat and Harrington, 2009). The ultimate objective of the male *Ae. aegypti* is to mate with and inseminate conspecific females. Thus, they are attracted to, and harbor at, human-based sites that attract females. Male *Ae. aegypti* are attracted to dark surfaces within and near premises, at oviposition sites, and around humans. Indeed, male *Ae. aegypti* are collected in large numbers by black target traps such as the Fay-Prince trap (Fay and Prince, 1970) and the BG Sentinel trap (Williams *et al.*, 2006). At these aggregation sites, males engage in a back-and-forth horizontal figure of eight flight usually less than 1-m high (Hartberg, 1971) across the upper face of the site. The active behavior of males exposes them to space-sprayed insecticides more than females, which typically remain quiescent (Reiter and Gubler, 1997). Males also conduct similar flights around the feet and lower legs of humans (Hartberg, 1971). These flights enable the male to rapidly detect, intercept and copulate with attracted females. Size and age of males is also important, as larger, older males have been shown to transfer more sperm during copulation (Ponlawat and Harrington, 2009). Interestingly, while it is possible to maintain male *Ae. aegypti* on a sucrose diet for many weeks under stable laboratory conditions, in the field limited evidence suggests that sugar feeding can be quite low, with values ranging from 11% to 29% (Edman *et al.*, 1992; Costero *et al.*, 1999; Spencer *et al.*, 2005). Unfed teneral males can out-survive unfed teneral females under field conditions, suggesting the importance of larval nutritional reserves (Costero *et al.*, 1999).

The Capacity to Migrate with Man

The capacity for *Ae. aegypti* to travel with man has also led to its success. All immature stages can travel in flooded containers, such as water drums on boats and ships (Tabachnick, 1991; Reiter, 2001; Shortus and Whelan, 2006). But as we have discussed, desiccation-resistant eggs can travel in dry containers; indeed, eggs on used automobile tires have been responsible for the mass global dispersion of the closely related *Ae. albopictus* in the late 20th century (Reiter and Sprenger, 1987; Benedict *et al.*, 2007). No doubt *Ae. aegypti* eggs have been similarly moved. Adult *Ae. aegypti* can also be transported in vehicles. I have witnessed female *Ae. aegypti* within automobiles and buses, and a case of ‘airport dengue’ was recently reported from near Darwin, Australia from the suspected transport of an infected female *Ae. aegypti* within a cargo plane from Indonesia (Whelan *et al.*, 2012). There have been three introductions of *Ae. aegypti* into the Northern Territory in recent years that have been the result of either transport of drought-resistant eggs in receptacles or adults in vehicles from Queensland or overseas (Whelan *et al.*, 2009). While the movement of adult *Ae. aegypti* in vehicles may be insufficient to create measurable gene flow (da Costa-Ribeiro *et al.*, 2007), it can contribute to the introduction of *Ae. aegypti* into new areas, and the potential spread of dengue virus.

MRR and population genetics studies have been used to identify local and regional barriers to dispersion and gene flow, respectively. On the local level, MRR studies demonstrated that female *Ae. aegypti* do not readily venture from urban into sylvan habitats (Maciel-de-Freitas *et al.*, 2006). As discussed previously, *Ae. aegypti* may be hesitant to cross busy roads (Russell *et al.*, 2005; Hemme *et al.*, 2010). None the less, human transport along roadways appears to play a significant role in dispersal and gene flow of *Ae. aegypti*. Populations of *Ae. aegypti* are panmictic along the Pacific coast of Mexico where several north–south roads allow significant car and truck traffic (Gorrochotegui-Escalante *et al.*, 2002). However, along the Gulf of Mexico, the Neovolcanic Axis creates an east–west barrier that is transected by only a single road. Populations of *Ae. aegypti* north and south of this barrier not only differ significantly in their genetic structure, but also in their vector competency for dengue virus (Lozano-Fuentes *et al.*, 2009). Smaller, isolated rural communities would also have restricted human traffic and, in the case of the outback towns of Charters Towers and Chillago, Queensland, have *Ae. aegypti* populations that are quite genetically distinct from coastal populations (Endersby *et al.*, 2011).

The Biogeography of *Ae. aegypti*: the Rise and Fall … and Rise of the '*aegypti* Empire'

Emigration of *Ae. aegypti* from Africa

Ae. aegypti originated in Africa from an ancestral sylvan form before becoming ecologically linked to man (Christophers, 1960; Tabachnick, 1991), and a hitchhiker as trade routes linked Africa to the New World and Southeast Asia. It is thought that the domestic form of *Ae. aegypti*, *Ae. aegypti aegypti*, diverged from the sylvan *Ae. ae. formosus*, when the climate of northern Africa began to dry around 2000 BC (Tabachnick, 1991; Brown *et al.*, 2011). At this time, dry weather would have forced humans to store water in leather and clay vessels, which would have selected for strains of *Ae. aegypti* that used these as oviposition sites. Furthermore, evolution of desiccation-resistant eggs would have allowed *Ae. aegypti* to travel in these containers even when dry. The trade routes from Africa into Southeast Asia and from western Africa into North and South America (particularly the slave trade) would have transported living *Ae. aegypti* colonies as immatures in water barrels, and as adult harboring and blood feeding within the dark confines of the ship. This led to the rapid expansion of *Ae. aegypti*, often accompanied by yellow fever virus, into areas where the mosquito (or the virus) did not occur. Genetic analysis of contemporary populations of *Ae. aegypti* suggest that multiple introductions of different African strains occurred (Brown *et al.*, 2011). Yellow fever outbreaks, vectored by *Ae. aegypti*, occurred in many urban centers in the eastern US seaboard such as Philadelphia and Boston (Reiter, 2001), suggesting that this species occurred in these northern latitudes, at least in summer. Indeed, in the mid to late 19th century, *Ae. aegypti* extended much further poleward in the major continents of the northern and southern hemisphere than it does currently. Paradoxically, this rapid expansion extended beyond the currently accepted 10°C winter daily mean isotherm climatic limit set by Christophers (1960).

How did this tropical insect suddenly appear in cities such as Philadelphia and Sydney and Athens where winter temperatures fall well below 10°C? While transport in water barrels on ships would have reintroduced *Ae. aegypti* to port cities during the summer (Gubler, 1997), Reiter (2001) states that some winter niches with temperatures above 0°C may have allowed *Ae. aegypti* to survive the harsh US winter. Eggs and larvae of *Ae. aegypti* may have persisted and overwintered in low numbers within subterranean wells and cisterns. Reticulated or piped water was not widely established in the 18th–19th centuries, and people utilized wells and cisterns to source and store water (Blake, 1956). Some of these were quite large (over 1000 liters), and wells, being insulated underground, did not freeze. These flooded subterranean containers have relatively warm temperatures, and can maintain eggs and even larvae despite subfreezing surface temperatures (Chandler, 1945). Eggs and larvae of *Ae. aegypti* may have survived the winter within internal cisterns (some were located under the house, as is seen in Key West, Florida), wells and water barrels (Chandler, 1945; Halstead, 2008). None the less, with the onset of warm weather in spring, physiological activity would resume and the house would soon be infested with *Ae. aegypti*. Ships would also have reintroduced *Ae. aegypti* into ports every spring and summer. Yellow fever virus would have been introduced by trade ships from infected areas such as the Caribbean, as was the case for Philadelphia (Powell, 1949). The major outbreaks of yellow fever and dengue in much of the eastern USA, Australia, the Mediterranean basin and South America in the 18th to early 20th century would have been the peak geographic range of *Ae. aegypti*.

The changing fortunes of *Ae. aegypti* in the 20th century

Blinded by science: changing demographics, architecture and eradication campaigns

The decline of the '*aegypti* empire' was heralded when Major Water Reed confirmed that *Ae. aegypti* was the vector of yellow fever virus. This finding ultimately spawned large eradication campaigns and changes in housing design (use of reticulated water, screening of houses) that dramatically reduced the range of *Ae. aegypti* in the 20th century. The eradication campaigns, characterized by large vertical programs that employed armies of disciplined workers, engaged in source reduction and use of the new residual pesticides such as DDT to spray water-holding containers that provided residual control of the vector (Reiter and Gubler, 1997; Reiter, 2007). Large vertical 'eradication' campaigns in North and South America, led by the energetic Fred Soper, were highly effective (Soper, 1963). Malaria eradication programs using DDT interior residual spraying also reduced *Ae. aegypti* in much of the Asia-Pacific region (Chow, 1967).

But a relaxation of funding and subsequent decrease in resources and collective will led to a resurgence of *Ae. aegypti* in the Americas after the 1970s (Gubler, 1997, 1998; Halstead, 2008). For an excellent review of the history of *Ae. aegypti* in the USA, see Eisen and Moore (2013). Destruction of water and sewage infrastructure, troop movements and increased urbanization led to increases in *Ae. aegypti* populations in post-Second World War Southeast Asia and the Pacific (Gubler, 1997, 1998; Herring and Swedlund, 2010). In Australia, the disappearance of *Ae. aegypti* from the southern half of the continent is thought to be due to a 'perfect storm' of factors simultaneously occurring after the Second World War: loss of urban rainwater tanks, use of residual pesticides in the home, community clean-up programs led by well-trained servicemen returning after the Second World War, and even the invention of the motorized lawn mower that encouraged citizens to maintain a tidy yard (Russell *et al.*, 2009). The loss of large water storage containers such as 5000–10,000-liter rainwater tanks is thought by Kearney *et al.* (2009) to explain the disappearance of *Ae. aegypti* in drier areas of Australia. Furthermore, the reintroduction of *Ae. aegypti* by steamships and steam trains was eliminated as road and air transport, being free of water-filled containers and thus mosquito-free, became dominant. In the USA, modern housing with piped water, screened windows and central air conditioning would have almost eliminated the domestic niche of *Ae. aegypti* in many regions. This is highlighted by the great disparity in dengue transmission between urban areas in Mexico vs. adjacent urban areas in Texas (Reiter *et al.*, 2003).

Interestingly, in the tropics increased urbanization, the reliance on water storage due to inadequate water supplies, and poor rubbish and waste removal (Gubler, 1998; Alirol *et al.*, 2011) have increased populations of *Ae. aegypti*. Large tropical mega cities such as Bangkok, Rio de Janeiro and Delhi have extensive slums with large populations of *Ae. aegypti* and dengue epidemics involving thousands of cases. As of 2008, 'The mosquito *Aedes aegypti* enjoys greater geographical distribution at present than at anytime in the past and is established in virtually all tropical countries' (Halstead, 2008, p. 274). Up until the mid-20th century, *Ae. albopictus* was the dominant container-exploiting mosquito in Southeast Asian cities (Gilotra *et al.*, 1967; Lambrechts *et al.*, 2010). That said, the former range of *Ae. aegypti* that included temperate zones well into North America and Europe has shrunk.

Competition with other exotic mosquitoes

The container-inhabiting mosquito *Ae. albopictus* has also contributed to the shrinking domain of *Ae. aegypti* in temperate areas. Nearly complete displacement of *Ae. aegypti* by *Ae. albopictus* has been observed throughout much of the southeastern USA (O'Meara *et al.*, 1995; Juliano and Lounibos, 2005), Guam, Hawaii, Saipan (Lambrechts *et al.*, 2010) and in the outer islands of the Torres Strait (S.A. Ritchie and J. Davis, Queensland Health, unpublished data). The 'Asian Tiger Mosquito', *Ae. albopictus*, also uses artificial and natural containers for larval habitat, but is generally more peridomestic than *Ae. aegypti* (Hawley, 1988). Thus it prefers lush vegetated areas over domesticated urban landscapes that harbor *Ae. aegypti*, and it is more common outdoors than indoors, although there is evidence that in some areas *Ae. albopictus* is becoming endophilic in response to increased urbanization (Wu *et al*., 2010; Kumari *et al*., 2011). Indeed, in some highly urbanized areas in the southeastern USA (such as New Orleans), *Ae. aegypti* persists, coexisting with *Ae. albopictus* (Juliano and Lounibos, 2005). *Ae. albopictus* is a generalist blood feeder, with many mammals such as man, dogs, cats, etc. the primary host (Hawley, 1988). In short, it is not as tightly linked to man as is *Ae. aegypti*, and can be found in numbers in sylvan areas away from man. While it is an important vector of several arboviruses such as chikungunya virus and the dengue viruses, it is not generally associated with explosive urban epidemics of dengue as is *Ae. aegypti* (Gubler, 1987; Lambrechts *et al*., 2010). However, in the last three decades, it has shown great capacity to invade and establish in new areas and countries, not unlike the spread of *Ae. aegypti* centuries before (Benedict *et al*., 2007).

Several mechanisms have been proposed to account for the displacement of *Ae. aegypti* by *Ae. albopictus*. The most attention has been on interspecific competition between larvae within containers. Laboratory studies using different densities and ratios of *Ae. albopictus* and *Ae. aegypti* have been conducted to measure the relative production of each species (Murrell and Juliano, 2008). In most instances, *Ae. albopictus* 'outcompetes' *Ae. aegypti*, with a majority of pupae produced being *Ae. albopictus*. Other factors shown to influence the relative survival of these two mosquitoes include detritus type (Murrell and Juliano, 2008), desiccation resistance of eggs (Juliano *et al*., 2002), and satyrism-induced infertility. In satyrism, male *Ae. albopictus* copulate with and inseminate female *Ae. aegypti*, and male accessory gland fluid then blocks sperm from subsequent matings from entering the spermatheca, rendering the females sterile (Nasci *et al*., 1989; Tripet *et al*., 2011). This has been proposed as the primary mechanism for rapid displacement of *Ae. aegypti* observed in places such as Africa and the USA (Tripet *et al*., 2011; Bargielowski *et al*., 2013). The relative success of adult females to blood feed to repletion could also directly affect fecundity. The catholic feeding habitats and outdoor preference ('exophilic') of *Ae. albopictus* (Hawley, 1988) could place it at a great advantage over *Ae. aegypti*, especially in areas where populations of domestic animals in the yard is high, and access to humans is limited by window screening and pesticide and repellent use. Clearly, it is more difficult for a female *Ae. aegypti* to blood feed on man in suburban screened houses in north Florida than it is for *Ae. albopictus* to feed on a dog in the yard. Interestingly, despite being introduced at a comparable time as it was introduced in the USA, *Ae. albopictus* co-exists with *Ae. aegypti* in much of Brazil (Braks *et al*., 2003; Prophiro *et al*., 2011). Braks *et al*. (2003) found that the Brazilian strain of *Ae. albopictus* is a superior larval competitor to *Ae. aegypti* when exploiting leaf litter resources in containers. Perhaps differences in housing, and better access to humans in unscreened premises, have given *Ae. aegypti* a competitive advantage in Brazil that is lacking in the USA. That said, coexistence of *Ae. aegypti* and *Ae. albopictus* can be found in much of Southeast Asia, further highlighting the complexity of interaction between these two species (Chung and Pang, 2002; Wu *et al*., 2010; Kumari *et al*., 2011).

An Australian Example of the Changing Fortunes of *Ae. aegypti*

I shall use an example from Australia, where the potential impact of climate change on dengue has been newsworthy. Australia has had a long history of dengue outbreaks since the 19th century. Indeed, the first published description of dengue hemorrhagic fever was published by Australian physician F.E. Hare during a dengue outbreak in 1897 in the goldmining town of Charters Towers, in outback Queensland (McBride *et al*., 1998). *Ae. aegypti* was widespread in coastal communities along the west and east coasts of Australia, ranging as far south as Melbourne in the east and just south of Perth in the west (Russell *et al.*, 2009). Sporadic dengue outbreaks, some of epidemic proportions, were not uncommon in urban areas. Indeed, large outbreaks occurred in New South Wales in the 1920s and in Brisbane and much of coastal Queensland in the 1940s (Lee *et al.*, 1982; Kay *et al.*, 1984). As discussed earlier, the geographical range of *Ae. aegypti* then contracted sharply after the Second World War – due to a range of factors that are touched on above and in more detail in Russell *et al.* (2009), Beebe *et al.* (2009) and Jansen and Beebe (2010). Dengue outbreaks similarly disappeared, with a hiatus of 26 years between an epidemic in Townsville in 1955 and one in the Torres Strait in 1981 (Kay *et al.*, 1984). The dengue vector *Ae. aegypti* is now restricted to northeastern Queensland. With the development of Cairns, Queensland as an international transit hub and tourist destination, the number of international arrivals increased to over 500,000 per year. Concurrently, the number of viremic dengue importations and outbreaks has risen sharply (from ca. 10/year to 30/year), especially in the last 5 years, when both dengue imports and outbreaks rose alarmingly despite a relatively unchanged rate of international arrivals (Ritchie, 2009).

What impact will climate change have on *Ae. aegypti* and dengue in Australia? Obviously, the model projections indicate the range of *Ae. aegypti* and dengue risk will spread south, approaching its old historic distribution (Hales *et al.*, 2002; Russell *et al.*, 2009). But a series of droughts in eastern Australia in the late 1990s and early 2000s, much of it El Niño-linked, led to severe water restrictions and changes in urban planning in cities such as Brisbane, Queensland. Water hoarding increased, with some residents modifying plastic bins and buckets to collect and store water for garden use. Rainwater tanks were constructed and added onto existing houses, and even mandatory for new housing. Thus, there was a ‘back to the future’ fear that Brisbane would soon see the re-establishment of *Ae. aegypti* if water hoarding became widespread and rainwater tank screens began to fail (Beebe *et al.*, 2009; Jansen and Beebe, 2010). This fear is not without merit. *Ae. aegypti* is located in several small outback communities within 200 km of Brisbane (Russell *et al.*, 2009), and has recently been re-introduced to parts of the Northern Territory (Tennant Creek) where it had been earlier eliminated. Furthermore, modeling studies suggested that rainwater tanks offer the sustained containerized water niche necessary for the establishment of *Ae. aegypti* in drier, cooler southern regions that include Brisbane (Kearney *et al.*, 2009; Williams *et al.*, 2010). Thus, the arrival of water tanks suggests that it may be only a matter of time before *Ae. aegypti* or *Ae. albopictus* become established in the large urban areas of southeast Australia (Beebe *et al.*, 2009; Jansen and Beebe, 2010).

The Future of *Ae. aegypti*: a Cloudy Forecast

Finally, what is the future of the ‘*aegypti* empire’? The rising importance of climate change research has resulted in several modeling studies and discussions about the potential impact of climate change and dengue, with an emphasis on the vector *Ae. aegypti*. Most studies have been based on the simplified approach projecting that the higher temperatures and water vapor pressure due to climate change would increase the area that could support *Ae. aegypti* (Patz *et al.*, 1998; Hales *et al.*, 2002). Furthermore, the epidemic potential within cities would increase as the extrinsic incubation period decreases in response to higher temperatures (Patz *et al.*, 1998). However, Gubler *et al.* argue that ‘models projecting potential epidemic transmission are sensitivity analyses only; human cases can not be determined since the models used in these studies are not fully parameterized and therefore cannot be used for regional predictions’ (2001, p. 229). Shorter time-scale influences such as El Niño can also result in above normal temperatures in many areas, which have been associated with an increase in dengue risk (Hales *et al.*, 1999; Corwin *et al.*, 2001). Banu *et al.* (2011), in a review of dengue in the Asia Pacific region, found an increased risk of dengue from climate change likely, but no evidence that it is currently happening. However, as we have seen, *Ae. aegypti* is tightly linked with artificial, domestic water-holding containers ranging from water storage tanks to discarded plastic ice cream containers. Thus, the impact of climate change will be much more complex than a simple increase in acceptable climate conditions based on temperature/rainfall alone, with political, economic and human activities playing a key role in the future distribution of *Ae. aegypti* (Reiter, 2001).

Clearly, man's response to climate change will define the changing range of *Ae. aegypti* in the future. We are currently in the midst of an invasion of exotic plants and animals driven by globalization (Hulme, 2009). Indeed, *Ae. aegypti* and *Cx. quinquefasciatus* were early globalization pioneers as they spread across the world on Spanish galleons and English barques. But today a range of exotic, container-inhabiting mosquitoes cloud the picture, including *Ae. albopictus* and *Ae. japonicas* (Juliano and Lounibos, 2005), as well as indigenous species such as *Ae. triseriatus* (USA) and *Ae. notoscriptus* (Australia) (Russell *et al.*, 2009). However, *Ae. aegypti* may be re-emerging in some areas, such as Florida, where it was recently displaced by *Ae. albopictus*. Low populations of *Ae. aegypti* have just reappeared in some Florida cemeteries where only *Ae. albopictus* has been collected in the past 20 years (P. Lounibos, unpublished data). Strong selection pressure against interspecific mating between *Ae. aegypti* and *Ae. albopictus* may also account for potential 're-emergence' of *Ae. aegypti* (Bargielowski *et al.*, 2013). Competition within resource-limited, water-filled containers, and the search for blood meals from humans protected by screens and insecticides, will likely continue to reduce the opportunities for *Ae. aegypti* in more westernized societies such as the USA, Australia and many parts of Southeast Asia and South America. Indeed, in the USA and Australia, *Ae. aegypti* has become a niche player where populations are concentrated in warm regions with open, unscreened colonial-style houses. Dengue outbreaks occur annually in the Cairns, Australia region (Ritchie, 2009), and autochthonous dengue transmission, centered in the old town area of Key West, Florida, occurred in two successive years, 2009–2010 (Graham *et al.*, 2011). Selection pressure from screened modern housing (Fig. 24.5) and other container-exploiting

Fig. 24.5. The changing architecture of dengue. *Ae. aegypti* are abundant, and dengue transmission concentrated, in the old, open 'Queenslander' houses in Cairns, Australia (Ritchie *et al.*, 2004; Hanna *et al.*, 2006). In many areas, older unscreened housing, in this case a wooden 'Queenslander' house, is being replaced by screened, air-conditioned apartment blocks that could greatly reduce dengue transmission.

mosquitoes may also force *Ae. aegypti* to evolve towards a more peridomestic form, not unlike its ancestral *Ae. aegypti formosus* in Africa. This accounts, in part, for the lack of dengue in some areas of the USA (Reiter *et al.*, 2003). Despite this, *Ae. aegypti* is opportunistic. High-rise urbanization does not eliminate it, nor associated dengue transmission as evidenced by continuing dengue transmission in Singapore (Ooi *et al.*, 2006). But in many tropical regions increased urbanization, overcrowding, lack of dependable water and poor housing are a serious issue and contribute to large dengue epidemics (Gubler, 2002, 2004). Indeed, projections indicate that urbanization will increase markedly in poorer areas of the tropics in the years ahead (Alirol *et al.*, 2011). Sea level rises in response to climate change could also increase immigration from coastal areas to inland cities in lowland areas such as Bangladesh and India (http://www.metoffice.gov.uk/climate-change/policy-relevant/obs-projections-impacts). No doubt domestic *Ae. aegypti*, and epidemic dengue transmission, will remain a serious problem in these areas.

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