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REVIEW ARTICLE

Critical review of the vector status of *Aedes albopictus*

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Abstract. The mosquito *Aedes* (*Stegomyia*) *albopictus* (Skuse) (Diptera: Culicidae), originally indigenous to South-east Asia, islands of the Western Pacific and Indian Ocean, has spread during recent decades to Africa, the mid-east, Europe and the Americas (north and south) after extending its range eastwards across Pacific islands during the early 20th century. The majority of introductions are apparently due to transportation of dormant eggs in tyres. Among public health authorities in the newly infested countries and those threatened with the introduction, there has been much concern that *Ae. albopictus* would lead to serious outbreaks of arbovirus diseases (*Ae. albopictus* is a competent vector for at least 22 arboviruses), notably dengue (all four serotypes) more commonly transmitted by *Aedes* (*Stegomyia*) *aegypti* (L.). Results of many laboratory studies have shown that many arboviruses are readily transmitted by *Ae. albopictus* to laboratory animals and birds, and have frequently been isolated from wild-caught mosquitoes of this species, particularly in the Americas. As *Ae. albopictus* continues to spread, displacing *Ae. aegypti* in some areas, and is anthropophilic throughout its range, it is important to review the literature and attempt to predict whether the medical risks are as great as have been expressed in scientific journals and the popular press. Examination of the extensive literature indicates that *Ae. albopictus* probably serves as a maintenance vector of dengue in rural areas of dengue-endemic countries of South-east Asia and Pacific islands. Also *Ae. albopictus* transmits dog heartworm *Dirofilaria immitis* (Leidy) (Spirurida: Onchocercidae) in South-east Asia, south-eastern U.S.A. and both *D. immitis* and *Dirofilaria repens* (Raillet & Henry) in Italy. Despite the frequent isolation of dengue viruses from wild-caught mosquitoes, there is no evidence that *Ae. albopictus* is an important urban vector of dengue, except in a limited number of countries where *Ae. aegypti* is absent, i.e. parts of China, the Seychelles, historically in Japan and most recently in Hawaii. Further research is needed on the dynamics of the interaction between *Ae. albopictus* and other *Stegomyia* species. Surveillance must also be maintained on the vectorial role of *Ae. albopictus* in countries endemic for dengue and other arboviruses (e.g. Chikungunya, EEE, Ross River, WNV, LaCrosse and other California group viruses), for which it would be competent and ecologically suited to serve as a bridge vector.

Key words. *Aedes aegypti*, *Ae. albopictus*, *Dirofilaria*, anthropophily, arboviruses, dengue, invasive species, spread of disease, vector competence, vector control, virus surveillance, zoonoses.

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Introduction

Over the last two decades *Aedes albopictus* has spread from the western Pacific and South-east Asia to Europe, Africa, the Middle East, north and South America and the Caribbean. Much attention has been devoted to this species both in the scientific literature and the popular press. Commonly referred to as the 'Tiger mosquito', its introduction into countries in which it has not been previously found is commonly considered as a serious threat and it is viewed as a potential or actual vector of arboviruses and other infections such as *Dirofilaria immitis*. Since its first finding in Albania in 1979 (Adhami & Murati, 1987), then its importation into the U.S.A. sometime before 1980 (Sprenger & Wuithiranyagool, 1986), the species has been reported from Belgium, France, Italy and Switzerland in Europe, from Israel in the Middle East, and from Cameroon, Equatorial Guinea and Nigeria in Africa. It is now widespread in the U.S.A., Central and South America. In Italy, it has become the most serious pest mosquito species through most of its range (Romi, 2001). Because of its spread to areas in which it has not been previously found and its high population densities in newly invaded areas, it is timely to review the extent to which this species is or may be a disease vector both in those countries in which it has long been present and those into which it has been introduced. This information is important to public health authorities as a guide in making decisions as to what priority and resources which should be allocated for control of this species.

Shroyer (1986) reviewed the literature on the relationship of *Ae. albopictus* to arboviruses; a further review was made by Mitchell (1995a). Since that time, the species has spread still more widely and considerable additional information has become available on its possible role as a vector of human disease. Knudsen (1995) stated that '*Ae. albopictus* ranks second only to *Ae. aegypti* in importance to man as a vector of dengue and dengue haemorrhagic fever'. In light of the continuing spread of the species, as well as the increasing incidence of dengue and other mosquito-borne arboviruses, it is essential to determine just what is known about the actual role of *Ae. albopictus* as a vector and therefore the magnitude of the effort that must be devoted to its control. The following article reviews information pertaining to the role of the species as an actual or potential vector of human disease.

In undertaking this review, the criteria outlined by Mitchell (1995b) for incriminating a species as a vector of arboviruses have been kept in mind; these are: (1) isolation of a specific virus from specimens collected in nature; (2) demonstration of infection in the mosquito following experimental feeding on a viraemic host or virus suspension; (3) demonstration of transmission of virus by bite to a vertebrate host or demonstration of virus in expressed salivary fluids; (4) field evidence confirming association of the mosquito species with the vertebrate population in which the virus infection is occurring. An earlier comprehensive definition of vector competence cited by Mitchell (1983) states 'the combined effect of all of the physiological and ecological factors of vector, host, pathogen, and environment that determine the vector status of a given arthropod population'.

Reports of *Aedes albopictus* as a vector in the early 20th century

Aedes albopictus was first described as 'the banded mosquito of Bengal' by Skuse (1894) from Calcutta, India (Huang, 1968; Knight & Stone, 1977). In the early literature, this mosquito was reported as a vector of dengue in several incidences, although no isolations of dengue were reported from *Ae. albopictus* before the Second World War. However, epidemic outbreaks of dengue in the absence of *Ae. aegypti*, but in the presence of *Ae. albopictus*, were deemed to warrant the conclusion that the latter species was the vector. In August 1942 a large dengue outbreak occurred in the port city of Nagasaki, Kyushu, Japan. It soon spread to other cities, recurring every summer until 1944. This was not only the first dengue epidemic in Japan proper but also one of the most widespread dengue epidemics recorded in a temperate region, involving at least 200 000 cases. Hotta (1998) considered that the principal vector was *Ae. albopictus*, which is found in the main islands of Japan, particularly south of 38–39° N. At that time an important factor in the transmission of infection was the large number of water tanks that had been set up in all cities for use against fires resulting from bombardments during the war. Other epidemics of dengue followed in Sasebo, Hiroshima, Kure, Kobe and Osaka cities and continued until 1944. After the Nagasaki outbreak in 1942, the epidemics in different areas probably arose independently through repeated introductions of the virus. It appeared likely that dengue fever patients among crew members of warships returning to Japan from South-east Asia were the means by which the virus was introduced to Japan and epidemics were sustained by *Ae. albopictus* in the cities into which the virus had been introduced. It also appeared that transmission of dengue occurred during the return of ships to Japan as evidenced by detection of the presence of *Ae. aegypti* on board ships. Limited populations of *Ae. aegypti* may have been present as an introduced species in Japan but were not thought to be responsible for dengue transmission during the epidemic except aboard ships. Investigators were sent to Nagasaki in early September 1942 to investigate the entomological aspects of the ongoing epidemic of dengue. They inspected a ship which had arrived in Nagasaki on 4 July 1942 after a protracted stay in a Thai port. The first two cases of dengue had been reported in the city on 11 July 1942. They found breeding of *Ae. aegypti* on board the vessel. They conducted a survey of the city but found only *Ae. albopictus*, which they believed was responsible for the transmission; they did not believe that *Ae. aegypti* had established itself in Nagasaki (Yamada *et al*., 1943). Gray (1947) stated that *Aedes togoi* was also a vector of dengue at the time. In a more recent review, Kobayashi (2002) states that *Ae. albopictus* was a vector of dengue in Japan at the time of the war-time epidemics.

In July 1943 a large outbreak of dengue occurred in Honolulu, Hawaii, which was reported as being introduced by pilots coming from Fiji. Earlier epidemics of dengue had occurred in Hawaii in 1902 and 1912. At the time of the

1943 epidemic, 85% of the *Aedes* mosquitoes of Honolulu were *Ae. albopictus* and 15% *Ae. aegypti*. Both were found as urban breeders but *Ae. albopictus* was also found breeding in tree holes and up to 2000 feet altitude. The breeding index in the city of Honolulu in September 1943 was 83% in a district with high rainfall and less than 4% in a dry area (Usinger, 1944). Gilbertson (1945) considered that *Ae. albopictus* was undoubtedly the vector during the Hawaiian epidemic but considered it to be less efficient than *Ae. aegypti*.

Reports of *Ae. albopictus* as a vector after 1945

Epidemics of dengue occurred in New Caledonia, New Hebrides and the Solomon Islands both during the 1940s war and thereafter. A review of the vectors in 1948 concluded that transmission only occurred where *Ae. aegypti* was present (Perry, 1948). In 1952, there was an outbreak of dengue in Assam, India in an area where dengue had not been previously recognized. The report states that *Ae. albopictus* was the 'proven' vector but provides no evidence for this (Birks, 1952). Elsewhere in India, Reuben *et al.* (1988) reported an isolate of dengue from *Ae. albopictus* in West Bengal, while Varma (1960) demonstrated its vector competence for the Tamil Nadu strain of West Nile Virus (WNV). Reeves (1959), in a review of mosquito-borne diseases in Indonesia observes that there are no control measures being undertaken against the vectors of dengue, which were reported to be *Ae. aegypti* and *Ae. albopictus*. By 1960, the epidemic of dengue/dengue haemorrhagic fever (DHF) which had started in Manila in 1954 had reached Bangkok, but Rudnick *et al.* (1960), who had carried out a mosquito survey in Bangkok, had found no *Ae. aegypti* in the city despite the high incidence of dengue/DHF in Bangkok. In 1964, Rao reviewed the status of the vectors of dengue and chikungunya in India (Rao, 1964). He observed that there appeared to be little information on the prevalence and bionomics of the species in that country, but thought that *Ae. aegypti* was probably the vector but that the possible role of *Ae. albopictus* should not be overlooked.

Dengue is a major public health problem in Cambodia: *Ae. aegypti* is considered to be the major vector and its densities are high through the country.

Russell *et al.* (1969) carried out a survey of dengue vectors or potential vectors in South Vietnam. Thirty strains of dengue were recovered from 46 862 *Ae. aegypti* collected in or near homes of patients with DHF. All four dengue serotypes were recovered. However, no viruses were recovered from any of the 8006 *Ae. albopictus* tested.

Surtees (1970) studied the distribution of mosquito breeding in the Kuching area, Sarawak, Malaysia. He found *Ae. aegypti* breeding in the city of Kuching and up to 16 km to the south of the city, whereas *Ae. albopictus* was the dominant species breeding in domestic containers in close association with man in all localities surveyed. From these observations he concluded that endemic dengue in Kuching is maintained in the human population by *Ae. albopictus*, although no virus isolation studies were made. Huang (1979) listed isolates of Reovirus 3 and Tembus Virus by Rudnick (unpublished data) in Malaysia. Knudsen (1977) described a silent 'jungle cycle' of dengue in Malaysia which involved *Ae. albopictus* and, possibly, other species of mosquitoes. From all the data obtained it was concluded that the transmission cycle is brought about by infected monkeys that have no symptoms or before they have appeared moving outwards from the centre of the forest and being fed on by females of *Ae. albopictus*. These mosquitoes then bite healthy monkeys with a range nearer the periphery of the forest, the cycle being repeated until a mosquito infected by a monkey at the forest edge bites a man working in a rubber or oil-palm plantation adjoining the forest. A few days later he is sick and stays at home, where he may be bitten by another *Ae. albopictus*, which infects other people in the village or returns to the forest to recommence the jungle cycle.

Elliot (1980) observed that surveys of mosquitoes in the South Pacific up until 1977 had shown the presence of *Ae. albopictus* only as far east as Papua New Guinea. However, during a visit to the Solomon Islands in 1978 to collect members of the *Aedes* (*Stegomyia*) *scutellaris* complex, he found *Ae. albopictus* in large numbers on Guadalcanal, and the species was also present in the Santa Cruz Islands. In his paper, the observation is made that this species has been incriminated as a vector of dengue haemorrhagic fever.

In 1978, dengue was reported in China for the first time in 32 years (Wufang Fan & Cosgriff, 1989). Since then, epidemics involving hundreds of thousands of people have occurred in Guangdong and Guangxi provinces and on Hainan Island. These epidemics were caused by all four types of dengue virus. *Aedes aegypti* was reported as the vector in coastal areas, whereas *Ae. albopictus* was named as the vector in inland regions.

Studies on the detection of dengue virus in mosquitoes by the intracytoplasmic specific fluorescence technique used for DEN-4 demonstrated dengue in 8 out of 21 head imprints and 5 out of 82 salivary gland, stomach and ovary imprints of female *Ae. albopictus* captured from the Fonshan district of Guangdong Province in 1978, and indicated that *Ae. albopictus* was the vector of the outbreak in that province (Qiu Fuxi *et al.*, 1981). Further studies in Guangdong Province were carried out by Wen & Du Liang (1998), who attempted virus isolates from nine species of mosquitoes. The positive rate of virus isolation in *Ae. albopictus* was 20.69%, in *Ae. aegypti* 18.95%, in *Cx. quinquefasciatus* 10.29%. Dengue viruses were not isolated in six other species of mosquitoes. The positive rate of virus isolation in the three species showed no significant differences. The authors concluded that *Ae. aegypti* was the main transmitting vector in Hainan Island and Zhanjiang District, whereas *Ae. albopictus* was the main transmitting vector in the other epidemic areas. Shortly thereafter, Chen (1982) reported the isolation of DEN-3 from *Ae. albopictus* on Hainan island.

One of the most unequivocal observations on the status of *Ae. albopictus* as a vector in China was made by Tang *et al.* (1988). In a review of the dengue outbreak in Guangxi Zhuang Autonomous region, they stated that both *Ae. aegypti* and *Ae. albopictus* have proven to be important vectors as shown by epidemiological studies, isolations and experimental infections. In China, *Ae. aegypti* is found only in certain coastal regions south of 22° latitude, but *Ae. albopictus* is much more widespread. In the 1980 and 1985 outbreaks on Hainan Island most cases appeared in coastal areas where *Ae. aegypti* is common. In the outbreaks in Guangdong where *Ae. aegypti* is absent, *Ae. albopictus* is the vector. All four DEN serotypes have been isolated from both species. DEN-4 has been isolated from *Ae. albopictus* in Yunnan province, where so far no dengue cases have been reported. In short, *Ae. aegypti* is the more important vector but *Ae. albopictus* is probably important in the maintenance of the infection. Isolations have been made in China from *Cx. quinquefasciatus* but its role as possible vector was considered quite uncertain.

Experimental transmission studies were carried out by Zhang & He (1989). The comparative susceptibility to dengue serotype 1, 2 and 4 virus infection of nine geographical strains of *Ae. albopictus* was studied by means of experimental feeding of the mosquitoes on pledgets soaked with virus–erythrocyte suspension and intrathoracic inoculation with dengue viruses. Variation in susceptibility for both dengue serotypes 1 and 2 was found among the geographical strains by feeding, but no significant difference among those by intrathoracic inoculation. It was evident that a 'gut barrier' was involved. Thresholds of oral infection were not the same for dengue serotypes 1, 2 and 4. In terms of infection rate, Haikou strain was more susceptible to all three serotypes of virus; Beijing and Chengdu strains were more susceptible to serotypes 1 and 2, respectively. All the geographical strains were more susceptible to dengue serotype 2 compared with the other two serotypes.

From the above and other studies not cited, it is evident that dengue virus is frequently isolated from *Ae. albopictus* in China; consequently, most Chinese authors consider it to be the primary vector, particularly in those areas where *Ae. aegypti* is not found or is uncommon, and a secondary or maintenance vector in other areas.

Both *Ae. aegypti* and *Ae. albopictus* are among the most common species of mosquitoes throughout this region, as is dengue and its DHF and DSS syndromes. Vazeille *et al.* (2003) observed that during the 1950s, the former principal vector of dengue viruses in Asia, *Ae. albopictus*, was replaced by *Ae. aegypti* in most major cities of the area. *Aedes aegypti* is now considered to be the main vector of dengue viruses in Asia. However, this mosquito has been described as having a relatively low oral receptivity for dengue viruses compared with *Ae. albopictus*. A study was made by these authors comparing the relative oral receptivities of *Ae. aegypti* and *Ae. albopictus* collected in south-east Asia from both sympatric and allopatric breeding sites. In all instances, the oral receptivity of *Ae. aegypti* to the dengue type 2 virus used was significantly higher than that of *Ae. albopictus*. The relative oral receptivity of *Ae. aegypti* and *Ae. albopictus* for two other low-passage strains of dengue 2 was also compared. In all instances, *Ae. aegypti* was significantly more receptive than *Ae. albopictus*, with a difference found only for a recently collected strain of *Ae. albopictus* collected from the field (Ta Promh strain, Cambodia, 2001). The authors also noted that there was a significant increase in the infection rate of *Ae. albopictus* of the Ta Promh strain with increasing generations in the laboratory, demonstrating the importance of considering the colonization history of mosquitoes when assessing their susceptibility to infection with dengue. The authors posed the question of whether *Ae. aegypti* should be held responsible for the emergence of dengue haemorrhagic fever; they concluded that *Ae. albopictus* populations now present in South-east Asia are less susceptible to infection with dengue type 2 virus than are *Ae. aegypti* populations. This result is supported by another study showing that both infection and transmission rates for dengue type 1 were higher for *Ae. aegypti* than for *Ae. albopictus* in Taiwan (Chen *et al.*, 1993).

Vazeille *et al.* (2003) further noted that *Ae. aegypti* does not transmit the virus vertically to its progeny very efficiently and thus may not contribute to the maintenance of the virus during interepidemic periods. On the other hand, *Ae. albopictus*, which is not highly orally receptive to dengue type 2 virus, is present mainly in rural areas and does not feed exclusively on humans. Male *Ae. albopictus* can transmit dengue virus sexually in the course of mating, and females can transmit it vertically more efficiently than can *Ae. aegypti* females. These two mechanisms could explain the maintenance of the virus in nature between epidemics in non-endemic areas where susceptible human or primate populations are not always present. *Aedes albopictus* also could bridge a putative sylvatic and an urban cycle of dengue, because it colonizes both rural and peri-urban breeding sites. The authors pointed out that even when the only vector present is *Ae. albopictus*, it can be responsible for dengue epidemics, as was shown for the outbreaks in the Seychelles and Japan, and the recent small outbreak in Hawaii (2001). They stressed that all *Ae. aegypti* in the study reported here were *Ae. aegypti aegypti,* the light domestic form. When they compared *Ae. aegypti formosus* (dark sylvatic form) from Madagascar with sympatric *Ae. albopictus*, they found opposite results, i.e. a much higher oral receptivity for *Ae. albopictus* for dengue type 2 virus. On this island, *Ae. aegypti formosus* is scarce and found only in rural breeding sites, whereas *Ae. albopictus* is the species encountered in cities.

Prompted by the appearance and rapid spread of DHF in Thailand, Scanlon in 1963 carried out a country-wide survey of *Ae. aegypti* distribution and bionomics (Scanlon, 1965). *Aedes aegypti* was found in virtually every settlement in the country. He deemed the eradication of dengue virus from Thailand to be impossible due to the presence of a native species of mosquito, *Ae. albopictus*, 'which is an effective laboratory vector of dengue virus and has been implicated on epidemiological grounds'. He also considered it possible that a sylvan cycle of dengue exists with *Ae. albopictus* as the vector. Furthermore, whereas *Ae. aegypti* breeding appeared to be restricted to lower altitudes, *Ae. albopictus* was found at all levels from the valley floor up to the top of the mountain peak at some 4500 feet above sea level. A study of the host preference of *Ae. albopictus* on the island of Koe Samui in southern Thailand found that that non-human sources represent the majority of *Ae. albopictus* bloodmeals (Sullivan *et al*., 1971), which would appear to lessen the vectorial capacity of the species in the area. However, Russell *et al*. (1969) had earlier carried out a survey on the presence of DEN-4 on the same island in 1967 and recovered 19 strains of DEN-4 from pools of *Ae. aegypti* and 10 from *Ae. albopictus*. A study on the laboratory transmission of dengue virus by both *Ae. aegypti* and *Ae. albopictus* was carried out in Thailand by Whitehead *et al*. (1971), who concluded that both species were highly susceptible to dengue infection.

Contrary to other observations, Watts *et al*. (1985) failed to detect natural transovarial transmission of dengue virus in *Ae. aegypti* from Bangkok or in *Ae. albopictus*. No virus was detected in suspensions prepared from 73 *Ae. aegypti* originating from eggs laid by three field-collected dengue 2 virus-infected mosquitoes. However, during the same period, DEN-2 virus was collected from 14 of 268 female *Ae. aegypti* collected in 8 of 35 houses. Dengue virus was not isolated from 1459 male and 1740 female *Ae. albopictus* or from 187 male and 505 female *Ae. aegypti* reared from immatures collected in Ban Yang, a village in which dengue was endemic. These data suggest that transovarial transmission was not an important maintenance mechanism during the study.

An extensive serological survey was carried out throughout Burma in 1973–1974 to detect antibodies to dengue and chikungunya in the country as well as the presence of mosquito vectors. The two viruses were found to be widespread throughout the country but no antibody to dengue nor chikungunya was detected in *Ae. aegypti*-free hilly areas (Thaung *et al*., 1975). On the other hand, Thaung (1978) considered that the outbreaks of dengue in the town of Lashio appeared to be associated only with *Ae. albopictus*.

In the course of entomological studies during an epidemic of DHF in central Java, Indonesia in 1978, both *Ae. aegypti* and *Ae. albopictus* were found to be widespread and common with the latter being the most abundant. Comparative studies on the vector competence of the two species showed that *Ae. albopictus* had a higher susceptibility than *Ae. aegypti* to oral infection with all four dengue serotypes. The two species were equally competent in transmitting the Bantul strain of dengue 3 virus after parenteral infection. The data suggest that *Ae. albopictus* could have been an important vector in this epidemic, but no direct observations were obtained to define the respective contribution of either *Ae. albopictus* or *Ae. aegypti* (Jumali *et al*., 1979). Tan *et al*. (1981) compared the growth of dengue virus in both species in Indonesia after parental injection and found that the growth curves in both were similar. The findings suggest that both species are equally competent in supporting dengue after parental infection. They concluded that *Ae. albopictus* may therefore play an important role in rural epidemics of dengue in Indonesia.

Both *Stegomyia* species are widely distributed throughout India. The yearly report of the National Institute for Viruses (NIV) in Pune for 1988 observes that *Ae. albopictus* is an important vector of dengue in south-east Asia and that DEN-4 virus has been isolated from it in Asanol, West Bengal by the NIV. Tandon & Raychoudhury (1998) stated that, in India, dengue is transmitted by *Ae. aegypti* in cities and *Ae. albopictus* in suburban and rural areas. Due to purported changes in the epidemiology of dengue in India, probably due to the invasion of suburban and urban areas by *Ae. aegypti* and *Ae. albopictus*, respectively, they conducted a study to determine whether *Ae. albopictus* (which they call 'the proven vector of dengue in suburban areas'), has gained a foothold in Calcutta. A larval and adult survey of *Aedes* species conducted from October 1995 to September 1996 in crowded areas of the city and an urban garden in the centre of the city found both *Ae. aegypti* and *Ae. albopictus* present in the surveyed areas as larvae and adults. *Aedes albopictus*, however, is competing with, and attempting to displace, *Ae. aegypti*.

Gokhale *et al*. (2001) carried out a study on the vertical transmission of DEN-2 by a strain of *Ae. albopictus* in India following intrathoracic inoculation of the virus; a total of 650 larvae and 1315 adults of the F1 generation obtained from *Ae. albopictus* were processed. One pool of larvae and two pools each of males and females showed the presence of DEN antigen. Pools of second and third gonotropic (G2 and G3, respectively) cycles were found positive for DEN virus. Filial infection rate was high in the progeny obtained from the batches of eggs (G2) which were stored at room temperature for 1–2 months as compared to the progeny obtained from the eggs which were allowed to hatch within 3–4 days. Six pools of 12 and seven pools of 11 showed the presence of DEN antigen in the batches of one and 2 months, respectively. This study indicates the capacity of the mosquito strains studied to effect vertical transmission and is comparable to similar studies elsewhere in Asia.

Tewari *et al*. (2004) carried out a 2-year study in three dengue endemic villages of southern India; *Ae. aegypti*, *Ae. albopictus* and *Ae. vittatus* were considered as the prevalent vector species. From 271 pools (4016 specimens) of adult females, eight dengue virus isolates were obtained, of which seven were from *Ae. aegypti* and one from *Ae. albopictus*. This is the first report of dengue isolation from *Ae. albopictus* in rural India. Infection rates in the two species were comparable. However, due to higher and perennial prevalence, *Ae. aegypti* is considered as primary vector, with *Ae. albopictus* playing a secondary role. Despite circulation of all four dengue serotypes detected mainly during the transmission season, the high anthropophilic index of the vectors and their abundance, no human dengue case was reported, suggesting silent dengue transmission.

A rather different approach to vector incrimination was taken by Ali *et al.* (2003) in Dhaka, Bangladesh. The authors found a spatial association between dengue case clusters and vector populations. Households reporting a recent dengue illness were more likely to have *Ae. albopictus* larvae present in the home when compared with households not reporting cases. Households reporting a recent dengue illness were also more likely to have a neighbour with *Ae. albopictus* present in the home. In contrast, the presence of *Ae. aegypti* within the premises as well as the homes of neighbours (within 50 m) was not associated with dengue illness. Given that the breeding habitats for *Ae. albopictus* are somewhat distinct from those of *Ae. aegypti*, the findings of this study were considered to have implications for control of dengue transmission in this urban setting, where much of the focus has been on indoor mosquito breeding and transmission.

Dengue/DHF is an important public health problem in Sri Lanka. Both *Ae. aegypti* and *Ae. albopictus* are widespread.

Between December 1976 and September 1977, an extensive epidemic of dengue type 2 occurred in the Seychelles, which infected some 75% of the population, although no cases of DHF were seen. Metselaar *et al.* (1980), who investigated the outbreak, stated that *Ae. albopictus* was the sole vector. Calisher *et al.* (1981) in their epidemiological investigation of this outbreak also stated that *Ae. albopictus* was the probable vector.

Aedes albopictus as a vector in its areas of recent expansion; Europe, the Americas, the Middle East and Africa

Before 1979, *Ae. albopictus* was widely spread in an area from the Pacific to Madagascar and the Seychelles in the Indian Ocean; in the north it was found in Beijing, China, Seoul, Korea and Sendai, Japan (Huang, 1979). In warmer areas it was found throughout most of the South-east Asia Region and west to Hawaii (Mitchell, 1995b).

However, in 1979 infestations of the species were found for the first time in Europe, in Albania, breeding in tyres in seven localities; it was thought to have been imported in tyres from China (Adhami & Murati, 1987). The initial infestation appeared to have been in a rubber factory adjacent to the port of Durres (Durazzo), from where the mosquito was shipped as eggs in tyres to recapping plants in other parts of the country. The special importance of this finding is that this is the first recorded infestation of *Ae. albopictus* outside Oriental and Australasian regions (Adhami & Reiter, 1998).

In September 1990, an infestation of *Ae. albopictus* was discovered in a school playground in the city of Genoa, Italy, where many tyres had been left to be used by the children for play (Sabatini *et al.*, 1990). Despite a long and severe winter season in 1990–1991, with temperatures below 0°, the species survived and scatter foci were found the following spring. It was considered that the species might become a permanent pest in Italy and a potential vector of arboviruses and *Dirofilaria* (Raineri *et al.*, 1991). Within a relatively short time both of these concerns were proven correct; *Ae. albopictus* appears to have found ideal environmental conditions for proliferating and extending its season of activity (Toma *et al.*, 2003). It has become the most important pest mosquito in Genoa and is the major biting pest through much of its range in Italy (Romi, 2001). Romi indicated that there was no evidence that the species was a vector of human disease in the Italy at the time of his paper. However, shortly thereafter, Cancrini *et al.* (2003b) detected the DNA of both *Dirofilaria repens* and *D. immitis* in a single *Ae. albopictus* collected in 2002 and considered that the species is a potential vector of both species of *Dirofilaria* in Italy. Cancrini *et al.* (2003a) carried out investigations in Padova town (Veneto region, NE Italy) to define the actual role of *Ae. albopictus* in the natural transmission of *Dirofilaria*. During summer 2000–2002, daytime captures were carried out. The presence of filarial parasites in mosquitoes was evaluated by PCR, and sequencing confirmed species assessment. DNA extraction was performed separately on pools of the insect abdomen and thorax-head, to discriminate between *Dirofilaria* infected/infective specimens. A total of 2721 mosquitoes were caught and *Ae. albopictus* was the most abundant species (2534). Filarial DNA belonging to *D. immitis* was found in 27.5% (19/69) of the abdomen pools of mosquitoes collected in summer 2000, and in 11.1% (16/144) and 4.9% (6/123) thorax-head pools sampled in 2001 and 2002, respectively. All studied areas harboured infective specimens. These results demonstrated that *Ae. albopictus* is a natural vector of *D. immitis* in Italy. The presence of the mosquito could affect the transmission pattern of canine heartworm disease in the urban environment and, considering the aggressive anthropophilic behaviour of the species (30–48 bites/h) in Padova, could enhance the circulation of filarial nematodes from animals to humans.

Elsewhere in Europe, *Ae. albopictus* has spread to France (Schaffner *et al.*, 2001) where it is now spreading, Belgium (unpublished reports), and a focus has been found in Serbia Minte Negro, Serbia (Petric, Report, and Flacio, Poster Report at 14th European SOVE Meeting Bellinzona, in Southern Switzerland in 2003). Other than the transmission of *D. repens* and *D. immitis* in Italy, there have been no reports of *Ae. albopictus* naturally infected with human disease agents in Europe, although concern remains high and close surveillance must be maintained.

Aedes albopictus in the Americas and its vector status

In 1985, breeding of *Ae. albopictus* was found for the first time in the U.S.A. in Harris County, Texas (Sprenger & Wuithiranyagool, 1986). Since that time it has spread very widely throughout eastern and central U.S.A. and in 2001 was found breeding in California (Linthicum *et al.*, 2003), where it may have become established after arriving from

China in standing water in plastic boxes containing the 'Lucky Bamboo' plant, *Dracaena* spp. The authors observed that while disease transmission has not as yet been associated with *Ae. albopictus* in the U.S.A., evidence suggests that the species may be implicated in the ecology of West Nile virus, based on the isolation of the virus from the species in nature (Turell *et al*., 2001). West Nile virus (WNV) has been isolated from the species in Pennsylvania (Holick *et al*., 2002). Kutz *et al*. (2003) found positive pools in the Baltimore–Washington area, suggesting a newly created enzootic focus for this virus, and believed that *Ae. albopictus* and *Ochlerotatus japonicus* Theobald, another species recently introduced into the U.S.A. and also found positive for WNV, could serve as bridge vectors from virus-infected birds. Vertical transmission of WNV in the laboratory has been demonstrated on several occasions but there is no indication for the time being of field transmission of this rapidly spreading arbovirus in the U.S.A.

Francy *et al*. (1990) reported that 10 strains of a new arbovirus belonging to the *Bunyamwera* group (Bunyaviridae) had been recovered from pools of (non-blood engorged) *Ae. albopictus* collected in a survey conducted in Potosi, Missouri, in August–September 1986. The name Potosi virus was proposed for the new virus. Alhtough there is no evidence that this virus causes illness in man, their evidence indicates that *Ae. albopictus* may serve as an arbovirus vector in the U.S.A. The urban–suburban distribution, aggressive behaviour, and broad viral susceptibility of *Ae. albopictus* may lead to the transmission of viruses of known public health importance and perhaps of viruses hitherto not transmitted to humans because of the feeding pattern of their usual vectors.

Further isolates of Potosi virus, as well as of Cache Valley and La Crosse virus, were made from *Ae. albopictus* (as well as from *Aedes triseriatus*) in Illinois in 1994–1995 (Mitchell *et al*., 1998) but the actual vectorial role of *Ae. albopictus* for these viruses remains to be elucidated. Fourteen strains of Eastern equine encephalitis (EEE) were isolated from 9350 *Ae. albopictus* in 96 mosquito pools in Florida in 1991; these are the first isolations of an arbovirus of public health importance from naturally infected albopictus in the U.S.A. since the species was discovered in the country in 1985 (Niebylsk *et al*., 1992). Although EEE is the least common arbovirus in the U.S.A., it has a high mortality rate (occasionally 30%) and the possible role of *Ae. albopictus* as a vector of this infection must be studied further (as indeed, is the case for all the isolations made from this species).

Two additional viruses have been isolated from the species in the U.S.A.; the first is a *Bunyamwera* virus, Tensaw virus, and the second a member of the California group of arboviruses, Keystone virus. Both of these viruses may be the cause of human disease but there is no indication that *Ae. albopictus* is a vector.

Gubler *et al*. (2001) summarized the vectorial status of *Ae. albopictus* as follows: 'Its potential importance in the United States is that it is an aggressive diurnal biter and could serve as a bridge vector for viruses such as La Crosse virus, EEE, and others, thus potentially increasing human risk to infection. Under experimental conditions, *Ae. albopictus* is a competent vector for 22 arboviruses, including all four dengue serotypes, yellow fever, Chikungunya and Ross River virus. Although there is still no direct evidence that *Ae. albopictus* transmits human disease in the United States, eight arboviruses, Cache Valley, Potosi, Tensaw, EEE, Keystone, Jamestown Canyon, LAC and WNV, have been isolated from this species. In 1997, the mosquito was detected in Peoria, Illinois, an area with long-term LAC transmission. Surveillance in Peoria showed that *Ae. albopictus* competed well against the resident mosquito species, *Aedes triseriatus*, but there was no evidence that *Ae. albopictus* transmitted LAC virus to humans. While the role of *Ae. albopictus* remains limited for the present in the continental U.S.A., this has apparently not been the case in the recent outbreak of dengue in Hawaii in 2001–2002.

Dengue fever has been documented in Hawaii for over 100 years, with major incidents occurring in 1852, 1856 and 1903. The last epidemic occurred during troop movements in 1943. Between 1992 and 2000, 18 cases of dengue were documented in Hawaii, all originating in foreign countries. The primary vector for dengue is *Ae. aegypti*, but it has not been found in the parts of Hawaii where transmission has occurred. Beginning in July 2001, there were 12 cases of imported dengue, but in August of the same year, a woman in the city of Nahiku, on the island of Maui, was diagnosed with dengue. She had not travelled outside Hawaii in many years. Dengue was later found in her family members, and the Maui Department of Health (DOH) issued a health warning to the island's population. Between 12 September 2001 and 30 April 2002, 1644 people across Hawaii were suspected of infections, and 76% of these people met Hawaii DOH criteria for further testing. By 3 April 122 cases of dengue infection had been confirmed. Seventy-five percent of these cases were on the island of Maui and 57% were in males, probably due to outdoor occupation. The origin of the virus was later traced to travel to Tahiti, which had experienced 40 000 cases of dengue. Isolates of the Hawaiian virus matched the Tahitian virus. The confirmed cases are probably due to multiple imports and endemic infections. The main vector in Hawaii appears to be *Ae. albopictus*. The city of Nahiku, which experienced the most infections, had dense populations of the mosquito. *Aedes aegypti* was eliminated from Maui in the 1940s and the main species in east Maui is *Ae. albopictus*.

Dog heartworm caused by the nematode *D. immitis* is a growing veterinary problem in the U.S.A. and an increasing number of human cases are being reported. In 1994, first-stage *Dirofilaria* larvae, probably *D. immitis*, were found infecting the Malpighian tubules in three of 163 *Ae. albopictus* collected from New Orleans, LA, which is the first report of a *Dirofilaria* infection in the U.S.A. in the species (Comiskey & Wesson, 1995). Shortly thereafter, an experimental transmission study showed that a small portion of the natural population of *Ae. albopictus* is susceptible to infection with *D. immitis* and that susceptibility may be increased rapidly by selection. The presence of developing *Dirofilaria* sp. larvae in the Malpighian tubules of field-caught females indicated that *Ae. albopictus* may be infected naturally with *D. immitis* in Florida (Nayar & Knight, 1999). In view of the veterinary importance of this nematode as a parasite of dogs and cats, as well as wild canids, in the U.S.A. and the increasing occurrence of infections in humans (Merrill *et al.*, 1980; Haddock, 1987), the finding that a species which is now as common as *Ae. albopictus* is an additional vector, especially one that so freely feeds on man, is of public health importance.

As would be expected, *Ae. albopictus* was soon found breeding close to the border with Texas in a tyre in Matamoros, Mexico in 1988. By 1993, the species was found in two of the northern states of Mexico (Ibanez Bernal & Martinez Campos, 1994). In 1995, large numbers of *Ae. albopictus* were captured during a dengue outbreak in Reynosa, Tamaulipas, Mexico. One pool of 10 *Ae. albopictus* males was positive for dengue virus: serotypes 2 and 3 were identified by serotype-specific monoclonal antibodies and confirmed by RT-PCR. This is the first report of *Ae. albopictus* naturally infected with dengue virus in America. Also, it is the very first time that *Ae. albopictus* males have been found infected with dengue virus in the wild (Ibanez Bernal *et al.*, 1997). The species continues to spread in Mexico, with an infestation reported from southern Chiapas State in 1993 (Casas Martinez & Torres Estrada, 2003).

Aedes albopictus was first reported in Brazil in 1986, in Rio de Janairio (Forattini, 1986) and in São Paulo State in September 1986 (de Brito *et al.*, 1986). The species is now present in 20 of the 27 states of Brazil (La Corte dos Santos, 2003). Kambhampati *et al.* (1991) analysed the genetic composition of the strains of *Ae. albopictus* from Brazil and the U.S.A. and compared them with those of several countries in the Western Pacific in order to trace the geographical origin of the invading mosquitoes. The US and the Brazilian populations were closest in terms of genetic distance from the Japanese populations. Based on discriminant and genetic distance analyses, the authors concluded that the US and Brazilian *Ae. albopictus* originated in Japan.

Inasmuch as both dengue and yellow fever are endemic in Brazil with a high incidence in many urban areas, there was concern with possible role of *Ae. albopictus* as a vector of these viruses. In a serological survey in Campos Altos City, in the state of Minas Gerais, a small number of cases of dengue were reported but no *Ae. aegypti* were found. A serological survey isolated DEN-1 from two pools of larvae of *Ae. albopictus* collected from old tyres. These are the first naturally infected larvae of *Ae. albopictus* found in Brazil. This finding was considered important as it suggests that methods of vector control directed against *Ae. aegypti* in urban areas may not eliminate dengue infections where *Ae. albopictus* is already established (Serufo *et al.*, 1993). With the eradication of *Ae. aegypti* from Brazil in 1954, urban yellow fever also disappeared from the country. However, *Ae. aegypti* was re-established in 1976–1997, the first cases of dengue appeared again in Brazil in 1982 and the infection is now the cause of major epidemics (more than half a million cases in Rio de Janerio in 2002). Yellow fever is transmitted by sylvatic species of vectors in forest areas of Brazil outside of the normal range of *Ae. aegypti*. Recently, *Ae. aegypti* was found in the southern part of Para State, considered to be the source of the main yellow fever epidemics (Mondet *et al.*, 1996). *Aedes albopictus* is also increasing its distribution especially in suburban zones. This species has a greater adaptive ability and represents an intermediate position between forest galleries where yellow fever circulates and urban agglomerations where *Ae. aegypti* is present. Mondet (2001) warns that the possibility of urban yellow fever now threatens Brazil. Concern was heightened with the finding of *Ae. albopictus* populations breeding in the rain forest near the urban area of Recife (State of Pernambuco) (Albuquerque *et al.*, 2000). The existence of *Ae. albopictus* in the metropolitan area of Recife as well poses a potential risk for the interaction of this mosquito species with the urban human population.

Massad *et al.* (2001) consider that the risk of urbanization of yellow fever in Brazil is actually imminent. They estimated the risk of an epidemic of urban yellow fever in a dengue-infested area by calculating the threshold in the basic reproduction number, R0, of dengue, above which any single sylvatic yellow fever-infected individual will trigger an urban yellow fever epidemic. They then analysed the relationship between the extrinsic incubation period and the duration of viremia, from which it is possible to define the R0 for dengue that would also suggest an outbreak potential for yellow fever and also calculated the critical proportion of people to vaccinate against yellow fever in order to prevent an epidemic in a dengue-endemic area. The theory proposed is illustrated by the case of Sao Paulo State in southern Brazil, where dengue is endemic and the risk of urban yellow fever is thus considered to be already imminent. This concern was heightened by the analysis of Mondet (2001), who observed that since the discovery of the sylvatic cycle of yellow fever in 1933, not only the extent of the epidemiological areas has changed, but also their limits. Ecological modifications that are currently taking place in the Amazon basin, which is an endemic reservoir of the virus, will inevitably facilitate and increase the contact between humans and vectors. While more and more urban areas harbour populations of *Ae. aegypti*, the domestic and urban vector of yellow fever, it is therefore particularly important to try to protect human populations living in emergence zones and epidemic areas and thus to prevent the arrival of the virus in towns with dense vector or potential vector populations via humans with viremia – in other words the much feared urbanization of yellow fever in Brazil.

However, Degallier *et al.* (2003) expressed a different view as to the vector potential of *Ae. albopictus* in Brazil for the transmission of dengue. They carried out a study in the state of Esprito Santo, where 60 500 cases of dengue were reported between 1995 and 1998. The purpose of the study was to determine whether *Ae. albopictus* was transmitting dengue virus in the locality of Vila Bethnia (Viana County),Vitria, ES. Of 37 *Ae. aegypti* and 200 *Ae. albopictus* adult mosquitoes collected and inoculated, DEN-1 virus was isolated only from a pool of two *Ae. aegypti* female mosquitoes. They believe that the study results suggest that *Ae. albopictus* still cannot be considered an inter-human vector in dengue epidemics in Brazil. No virus was isolated from either females or males or immature stages of either species and they considered that vertical transmission was not taking place in either species within their study area. Since the introduction of *Ae. albopictus* in Brazil, the vector potential of this species has remained a controversial issue. Recent evidence showed that dengue virus may be vertically transmitted by this species in nature but are of the opinion that no data were available on its man-to-man vector potential.

Thus, while the present evidence of the degree of vector competence of *Ae. albopictus* in Brazil remains uncertain, a study by Lourenco de Oliveira *et al.* (2003) on a population genetic analysis emphasized that there is a large genetic differentiation and low variation in vector competence for dengue and yellow fever viruses of *Ae. albopictus* from Brazil, the U.S.A. and the Cayman Islands and that infection rates with dengue and yellow fever viruses showed greater differences between two Brazilian samples than between the two North American samples or between a Brazilian sample and a North American sample. Introductions and establishments of new *Ae. albopictus* populations in the Americas are still in progress, shaping population genetic composition and potentially modifying both dengue and yellow fever transmission patterns. In short, the vector potential of this species, which continues to spread to new geographical and ecological areas, within the Americas, must be viewed as still in a formative stage. Nevertheless, the conclusions expressed by Lourenco de Oliveira *et al.* (2004) leave no room for complacency. After the completion of a population genetic analysis using isoenzyme variation combined with an evaluation of susceptibility to both yellow fever and dengue 2 viruses conducted among 23 *Ae. aegypti* samples from 13 Brazilian states, they showed that experimental infection rates of *Ae. aegypti* for both dengue and yellow fever viruses are high and heterogeneous, and samples collected in the endemic and transition areas of sylvatic yellow fever were highly susceptible to yellow fever virus. Boa Vista, a border city between Brazil and Venezuela, and Rio de Janeiro in the South-east region are considered as the most important entry points for dengue dissemination. Considering the high densities of *Ae. aegypti*, and its high susceptibility to dengue and yellow fever viruses, the risk of dengue epidemics and yellow fever urbanization in Brazil is more real than ever, although the role of *Ae. albopictus* with its increasingly dense urban populations remains, as stated above, uncertain. As no clear indication has as yet been seen incriminating *Ae. albopictus* as an arbovirus vector in the Americas, further studies are needed to ascertain what, if any, factors have so far prevented it from becoming a vector.

Aedes albopictus in continental Africa

In 1991, Cornel and Hunt reported finding living *Ae. albopictus* larvae in tyres imported from Japan in Cape Town, South Africa (Cornel & Hunt, 1991); they thought that it was quite possible that undiscovered infestations might be present elsewhere in Africa. Very shortly thereafter, the first report of a breeding population of *Ae. albopictus* was made from the Delta State region of Nigeria, Africa (CDC, 1991). Almost immediately thereafter another population was found in Benue State 255 km east north-east of the localities in Delta State (Savage *et al.*, 1992). It would seem likely that the species had been present for some time in Nigeria before the first finding of breeding populations.

In 1999, biting female *Ae. albopictus* were found for the first time in Southern Cameroon; this prompted a large-scale survey in 2000 and breeding populations and adults were found widely in five towns or cities in the south of the country, breeding mainly in old tyres. Tyres are frequently imported from both the U.S.A. and Nigeria, both of which are infested with the species (Fontenille & Toto, 2001).

Soon thereafter, *Ae. albopictus* populations were detected on Bioko Island for the first time in November 2001. It was found to be well established, breeding in artificial containers at Planta, near Malabo, the capital of Equatorial Guinea. As with the first findings of the species in South America, the authors expressed concern that *Ae. albopictus* might become a 'bridge vector' between rural or sylvan foci of yellow fever and other arboviruses and urban centres, as it breeds well both in forests and in cities (Toto *et al.*, 2003). The authors also predict that the species will be found elsewhere in sub-Saharan Africa and this seems all too likely. So far, there have been no isolations of disease agents from *Ae. albopictus* in the three countries in which it is known to have become established in Africa, but relatively few surveys have so far been carried out.

The control of *Aedes albopictus*

Aedes aegypti was eradicated from most of the countries of the Americas during the 1960s under the aegis of a vertical and relatively well funded eradication campaign backed by a high degree of political and community will. However, the high level of control and commitment could not be sustained and by today, every country which had achieved control has been reinfested; the species is now more widely distributed than prior to the eradication campaign. With the invasion of *Ae. albopictus*, both *Stegomyia* infestations are now common in both urban and rural areas. Despite the calls for another attempt to eradicate *Ae. aegypti*, neither eradication nor effective control is being achieved in most areas. The best approach at this juncture would be to improve mosquito abatement capabilities in urban areas and attempt to reduce vector densities to a level at which disease transmission is unlikely. Achieving the same level of trained staff and organization as at the time of the vertical eradication programmes does not seem feasible under present conditions. To obtain a level of vector mosquito control necessary to reduce the transmission of dengue and prevent the urbanization of yellow fever will require better funding and more training of vector control personnel than most of the countries in the Americas are now devoting to their control programmes. A small outbreak of urban yellow fever in Bolivia was contained only by rapid immunization (Van der Stuyft *et al.*, 1999). National and urban programmes must take into account the high costs associated with large epidemics of dengue and DHF and the threat of yellow fever and invest funding in the improvement of their vector control programmes and training of qualified personnel. The active cooperation of an educated community with the support of well-trained mosquito control staff will be the only effective and economically acceptable approach for the reduction of *Ae. albopictus* densities in suburban and rural areas.

Conclusions

The spread of *Aedes* (*Stegomyia*) *albopictus* from eastern Asia to Europe, North and South America and Africa has raised concern among public health authorities in all countries in which its presence has been recorded and in those countries threatened by introduction of the species. It is referred to in both scientific and popular literature as a vector of dengue, chikungunya and other arboviruses. As has been seen above, many different arboviruses have been isolated from the species. However, if one returns to the definition proposed by Mitchell *et al.* (1998), i.e. (1) Isolation of a specific virus from specimens collected in nature; (2) Demonstration of infection in the mosquito following experimental feeding on a viremic host or virus suspension; (3) Demonstration of transmission of virus by bite to a vertebrate host or demonstration of virus in expressed salivary fluids; (4) Field evidence confirming association of the mosquito species with the vertebrate population in which the virus infection is occurring', one finds that the number of locations which fit all of these criteria is relatively limited. Indeed, *Ae. albopictus* can be unequivocally incriminated as a vector of dengue only where transmission occurs in the absence of *Ae. aegypti* or any other potential vector. Such transmission in the absence of *Ae. aegypti* or other species of *Stegomyia*, has been seen to occur in parts of China, at one time in Japan and the Seychelles, most recently in Hawaii and possibly La Reunion Island in the Indian Ocean. In other areas, particularly in South-east Asia, it appears that *Ae. albopictus* serves primarily as a maintenance vector of dengue in rural areas. In some areas, such as Bangkok, Thailand, *Ae. albopictus* has been displaced by *Ae. aegypti*, and this has also occurred in parts of Florida, where there are reported declines in the populations of *Ae. aegypti* and *Ae. triseriatus* in the areas of greatest expansion of *Ae. albopictus* (O'Meara *et al.*, 1993). One of the reasons for the successful competition of *Ae. albopictus* against other container-breeding mosquitoes was shown by field experiments carried out by Juliano (1998) in south Florida. Contrary to previous laboratory experiments, *Ae. albopictus* was clearly the superior competitor in tyres maintaining positive population growth at higher combined density and lower per capita resource availability than did *Ae. aegypti*. The primary determinant of success in this experiment was survivorship to adulthood, and *Ae. aegypti* only survived well in this environment when raised alone at low density, with high resource availability. The author concluded that resource competition among larvae appears to be sufficient to account for replacement of *Ae. aegypti* by *Ae. albopictus* in suburban and rural areas of south Florida, which may have been marginal habitats for *Ae. aegypti*. Earlier, Black *et al.* (1989) reported that mosquito abatement workers in Houston, TX, and New Orleans, LA, have observed that the recent introduction of *Ae. albopictus* has been accompanied by a decline and virtual disappearance of *Ae. aegypti* and that this suggests competitive displacement but contradicts the direction of displacement observed in native habitats of *Ae. albopictus*. Generally, *Ae. albopictus* develops more readily in rural and suburban areas, where it readily breeds in natural habitats, whereas other than in Africa, *Ae. aegypti* is only occasionally found breeding in such natural habitats as tree holes and plant axils. Although there are instances of displacement of *Ae. aegypti*, the latter species is able to maintain itself and occasionally displace *Ae. albopictus* in urban areas. This supports the possibility that *Ae. albopictus* may serve as a rural, maintenance vector of arboviruses in rural areas. It must be emphasized, however, that the relationship between *Stegomyia* populations in most parts of the world appears to still be in a formative stage.

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